1960

Life history of Marsipometra hastata and the biology of its host, Polyodon spathula

Fred Paul Meyer
Iowa State University

LIFE HISTORY OF *MARSIPOMETRA HASTATA* AND THE BIOLOGY OF ITS HOST, *POLYODON SPATHULA*

by

Fred Paul Meyer

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Parasitology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1960

TABLE OF CONTENTS

INTRODUCTION

The paddlefish, Polyodon spathula (Walbaum, 1792) Rafinesque, 1820 is one of the most primitive of modern fresh-water fishes. It is a relic species from an ancient period and attracts much attention because of its paddle-like snout, shark-like shape, and large size. Polyodon occurs only in the Mississippi River drainage system of North America. Its only modern related form, Psephurus gladius, occurs in the Yangtze River of China. Little is known of the ecology, life history, food habits, or parasites of the paddlefish.

Although the cestode parasites of Polyodon have been recorded, previous attempts to elucidate their life cycles have been unsuccessful. Tapeworms of the genus Marsipometra commonly infect those paddlefish taken from areas of the Mississippi and Missouri Rivers adjacent to Iowa. Marsipometra hastata (Linton, 1898) Cooper, 1917 occurs in most paddlefish, but its life cycle has remained enigmatic. It is hoped that knowledge concerning the life cycle and developmental stages of this parasite, as presented in this study, will provide an insight into the evolution of, and aid in disclosing the relationships of the genus Marsipometra to more advanced groups of tapeworms.

The paddlefish was formerly abundant in the Mississippi Valley, but its numbers have been drastically reduced, perhaps by habitat deterioration, over-fishing, or both. Laws intended to help preserve the species have been passed by the legislatures of several states with varying degrees of success. Due to a lack of data collected by qualified scien-

tists, many of these laws are based upon incomplete evidence gathered from the observations of commercial fishermen. In recent years, with the construction of large impoundments on the Mississippi and Missouri Rivers, paddlefish are increasing. A renewed interest in Polyodon has arisen with the development of sport and commercial fisheries in these areas. It is hoped that the data presented herein will lead to a more complete knowledge of the biology of this valuable fish.

This study, therefore, involves two major phases: one dealing with the life cycle of the tapeworm, Marsipometra hastata, the other, concerning the biology of its paddlefish host, Polyodon spathula.

PART I. THE LIFE CYCLE OF *MARSIPOMETRA HASTATA* (LINTON, 1898) COOPER, 1917

REVIEW OF LITERATURE

The first description of a cestode parasite from the intestine of the paddlefish, Polyodon spathula, was that of Linton who, in 1898 published a morphological account of a species which he named Dibothrium hastatum. Linton's material was taken from fish collected in the Ohio River near Bellaire, Ohio, in March 1889. Following his description, only infrequent references were made concerning this parasite (Beach, 1902; Stockard, 1907). Cooper (1917) felt that the cestode could not belong in the genus Dibothrium and erected a new genus Marsipometra, to include the species hastata named by Linton (1898). Later, Cooper (1918) gave a more adequate description of the species and placed it into a new subfamily (Marsipometrinae) of the Diphyllobothriidae. In 1930, P. H. Simer began a comprehensive study of the cestode parasites of the paddlefish. Based upon materials collected from the Tallahatchie River near Money, Mississippi, Simer described two additional species, M. confusa and M. parva. Beaver and Simer (1940), in a later and more complete study, emended the diagnoses of the family Amphicotylidae and of the subfamily Marsipometrinae. In this report, they provided complete illustrations of the three species involved in their investigations.

Cooper (1918) erected the subfamily Marsipometrinae for the genus Marsipometra and placed it in the family Diphyllobothriidae Lühe 1910. In Cooper's study, the subfamily Amphicotylinae was included in the family Ptychobothriidae Lühe 1902. According to Wardle and McLeod (1952) Nybelin in 1922 erected the family Amphicotylidae and listed the

Amphicotylinae and Abothriinae as subfamilies. Although Cooper (1918) had earlier given subfamily rank to the Marsipometrinae, Nybelin refused to accept this group in the family Amphicotylidae. When the genus Marsipometra was restudied by Beaver and Simer (1940), they emended Nybelin's 1922 description of the family Amphicotylidae to include the subfamily Marsipometrinae. This phylogenetic designation has been accepted by Wardle and McLeod (1952) and by Yamaguti (1959). This study also follows the classification proposed by Beaver and Simer.

Tapeworms of the family Amphicotylidae are small to medium sized worms with unarmed scolices bearing distinct bothria. The segmentation of the strobila is complete, each proglottid bearing a single set of reproductive organs. Adult worms occur in the intestine of teleost fishes. Three subfamilies comprise the family, namely, the Amphicotylinae found in salmonid and centrarchid fishes, the Abothriinae in gadid and cyprinid fishes, and the Marsipometrinae which are limited exclusively to the paddlefish, Polyodon spathula. The subfamily Marsipometrinae includes but a single genus, Marsipometra, and is distinguished from the other subfamilies by a secondarily-lobed uterus, a well-formed seminal receptacle and by yolk glands restricted to the area of the longitudinal muscles.

Few of the life cycles of tapeworms included in the family Amphicotylidae have been elucidated. Eubothrium crassum, in the subfamily Amphicotylinae, utilizes species of Cyclops as well as Perca fluviatilis as intermediate hosts. Rosen (1918) reports that Abothrium infundibuliforme of the Abothriinae is capable of completing its life cycle without the use of a second intermediate host. Normally, however,

two intermediate hosts, a copepod and a small fish, are required. The first data on a life cycle of one of the Marsipometrinae are presented in this paper.

MATERIALS AND METHODS

Tapeworms used in this study were removed from paddlefish collected from two areas, namely Pool 19 of the Mississippi River near Burlington, Iowa and from the tailwaters of Fort Randall Dam located on the Missouri River near Pickstown, South Dakota. Collections from the Mississippi River were made during the months of September through May. Collections from the Missouri River were made only during the months of June, July, and August.

All fish taken at the Mississippi River were transported to a local fish market for examination. During the winter months, refrigeration was unnecessary. Fish collected in the summer were either refrigerated or kept alive while being transported from the field. At a local market, heads and viscera were removed, and tapeworms were then collected from the digestive tract. The cestodes were placed into physiological saline until they could be fixed. Following fixation in AFA, worms were stored in 70% ethyl alcohol.

Since tapeworms collected from frozen fish or from fish which had been dead for several hours showed distortions in the nature of their scolices and strobili, all worms included in this study were those removed from freshly killed fish or from fish which had been dead less than one hour. It became apparent that autolysis occurs quickly in the viscera of paddlefish. On a warm day, the viscera filled with gas and the flesh softened. Within three hours on such a day it was not unusual for the body wall to rupture under the pressure of the accumulated gases.

Worms migrated almost immediately after the death of the host and frequently appeared at the anal opening. It was found that they may also migrate from the gut and leave the body by way of the branchial region. Worms which had actually moved out of the body as well as those which were migrating in the digestive tract were often greatly distorted. Worms from the various regions were fixed in AFA for sectioning and for preparation of whole mounts. Cestodes taken, in early phases of the study for the purposes of securing eggs, were transported under several conditions to the laboratory. These conditions included worms in refrigerated, unchlorinated tap water, worms in tissue fluids under refrigeration, in situ in the viscera under refrigeration, and worms in saline. Of these four groups, only the latter two conditions permitted maintenance of the parasites with a minimum of distortion. Whenever live worms were needed, they were transported in physiological saline solution.

Whole mount preparations of Marsipometra hastata were made using various techniques. These included Mayer's paracarmine, Ranvier's picrocarmine with $KMnO_4$ and oxalic acid ($C_2H_2O_4$) decolorization, Van Cleave's double haemotoxylin technique, and Harris' haematoxylin. Fast green and eosin counterstains were frequently employed. Of the above techniques, Mayer's paracarmine with a slight fast green counterstain gave the most satisfactory results.

Worms sectioned at 8-15 microns were stained with Delafield's haematoxylin or with Heidenhain's iron haematoxylin and counterstained with eosin.

Experiments to determine hatching conditions involved collections of eggs from gravid worms within 24 hours after their arrival at the laboratory. During early experiments, worms were teased apart with dissecting needles to remove the uterus to obtain eggs. Later it was possible to collect naturally-shed eggs. These were stored in refrigerated natural water or in normal saline. A further discussion of these techniques may be found in the section concerning hatching.

Crustaceans used in early experimental work relating to intermediate hosts were secured from a biological supply house but were later collected from natural sources. Some insect larvae collected in nature were also used. Most specimens of crustaceans used were taken from Lake West Okoboji, Iowa or from the tailwaters of Fort Randall Dam, Pickstown, South Dakota. Collections of zooplankton were made using a No. 20 mesh Wisconsin plankton net towed at various depths to insure collection of the various species of microcrustaceans. These plankton forms were transferred to one-gallon aquaria and transported back to the laboratory. There the aquaria were placed under refrigeration to reduce the activity of the crustaceans which could then be concentrated and separated into individual groups with little difficulty. These groups, in turn, were re-cooled and further separated according to species insofar as was possible. Isolated species were placed into separate aquaria for rearing. Details of these techniques are discussed in a later section concerning intermediate hosts.

Copepods, cladocerans, and amphipods were identified using keys by Stromsten (1920a, 1920b), McDonald (1939), Pennak (1953), Eddy and

Hodson (1955), and Needham and Needham (1955). Identifications of fish were verified with the use of Iowa Fish and Fishing, Harlan and Speaker (1956).

Illustrations were prepared with the aid of the camera lucida unless otherwise noted.

SUMMARY OF THE LIFE CYCLE

Adult Marsipometra hastata in the intestine of Polyodon spathula begin to release eggs soon after the temperature of river water reaches 60°F. Hatching occurs immediately after the eggs are exposed to river water and ciliated onchospheres (coracidia) are released. These live for several days at 61°F. but their life span is considerably reduced at higher temperatures. If ingested by the intermediate host, Cyclops bicuspidatus, the onchospheres penetrate the wall of the intestine and reach the haemocoel eight hours after they are eaten. The developing larvae do not develop cercomers, neither do they form typical pseudophyllidean procercoid stages. Instead, they slowly assume the shape of plerocercoid larvae. After developing for 55 days, the cestodes attain a size and shape closely resembling the smallest stages recovered from the intestine of naturally-infected paddlefish. Attempts to complete the life cycle by feeding plerocercoids to laboratory-reared paddlefish have not been possible.

In nature, the life span of Marsipometra hastata in its definitive host, Polyodon spathula, is less than one year. Juvenile worms first become common in mid-August and continue to increase in number during the early fall. The proportion of adult cestodes to immature ones gradually increases throughout the winter and by mid-April nearly all of the worms are gravid. Egg-laying then commences and the number of cestodes drops sharply soon afterwards. In late June, adult worms are no longer common in the paddlefish and by late July, one rarely finds them. At that time, juvenile worms begin to appear in limited numbers.

ADULT WORMS

Morphology

Cooper (1917) established the genus Marsipometra to include pseudophyllidean cestodes found in the paddlefish, Polyodon spathula. His generic diagnosis was emended in 1940 by Beaver and Simer. The genus is characterized as follows:

Genus Marsipometra Cooper, 1917.

Elongate worms with distinct, regular external segmentation, margins serrate; proliferation zone present or absent. Scolex triangular to bell-shaped, with distinct apical disc set off by circumferential markings, and bearing two distinct, sometimes shallow, bothria. Cirrus and vaginal openings in genital atrium at mid-lateral margin of proglottid, irregularly alternating. Cirrus muscular and protrusile. Testes numerous, not continuous from proglottid to proglottid. Prostate gland present and medial to cirrus sac; seminal receptacle variable, sharply set off from vagina. Vitellaria external to circular muscles, in region of longitudinal muscles. Uterus sacculate, with numerous lobes; uterine pore ventral. Ovary large, reniform, tubulolobular, located in posterior one-third of proglottid.

According to the studies of Simer (1930) and of Beaver and Simer (1940), three distinct species of Marsipometra, namely, M. hastata, M. confusa, and M. parva, parasitize the paddlefish, Polyodon spathula. Despite the similarity in general appearance of these species, they were considered as distinct species on the basis of such features as nature

of the scolex, location of the uterine pore, number of lobes in the uterus, location of the ovary, development of the seminal receptacle, presence or absence of a seminal vesicle, and the size and number of testes. Included in the initial collection of worms used in my research was a variety of worms which did not correspond to any of the descriptions given by the above workers. It was later shown that these worms represented a single species, M. hastata, which had undergone distortion from the effects of various techniques of handling. As noted previously, worms which have been frozen, subjected to various fluids, or removed from dead fish are likely to exhibit alterations in their morphology. The scolex may swell and lose its deep bothria, the apical organ may lose its identity, and the nature of the strobila may be altered markedly. The scolex of a living worm shows a remarkable facility for changing its shape. It may be elongate and narrow, or short and bell-shaped. During active movement, it may exhibit a threefold increase in length with a corresponding decrease in diameter. Depending upon the state at which the worm is killed, many variations in the scolex may be produced. (See Fig. 9).

Marsipometra parva is easily distinguished from the other two species of the genus by its few large testes and the absence of a seminal vesicle. The differences said to exist between M. confusa and M. hastata are much less distinct however. According to Beaver and Simer (1940), these species may be separated from one another by differences in the depth of the genital atrium, the nature of the cirrus sac, lobation of the uterus, relative position of the uterine pore, and the number

of testes. Of these characteristics, many can be altered by the amount of flattening or pressure used when preparing the specimens for study, or may depend upon the state of contraction of the worm when fixed. The age of the worms involved may also affect the nature of these changes.

Studies of sectioned worms and of whole mounts indicate that the differences between Marsipometra hastata and the M. confusa of Beaver and Simer (1940) are less significant than they indicate. It has not been possible to collect fresh material from the area in which the holotypes were taken. However, these holotypes and additional syntypes are available and have been examined. Careful comparisons of this material with that collected in my study indicate that separation of M. hastata and M. confusa on the basis of the number of testes is difficult, and that scolex characters are invalid for taxonomic purposes since the condition of the host from which the cestodes are removed has a pronounced effect upon the morphology of the worms.

One of the major differences between Marsipometra hastata and M. confusa, presumably, is related to the number of testes. Beaver and Simer (1940) listed a range of from 130 to 150 testes in M. hastata and a range of 180 to 250 in the case of M. confusa. Examination of holotype material indicates that these limits are not clear and distinct. When data from my collections are included, the range in number of testes in M. hastata extends considerably beyond the described limits and overlaps the range given for M. confusa. In my studies, I have found a range of 138 to 205 testes for M. hastata, averaging 163 per proglottid (based on counts of three different proglottids from each

of 30 worms). This average of 163 testes is at considerable variance with the range of either M. hastata or M. confusa as suggested by Beaver and Simer (1940).

The arrangement of the testes is another character previously used in distinguishing between the two species. In Marsipometra hastata, the testes are said to be arranged in a single layer, whereas, in M. confusa, two or three indistinct layers occur. My studies indicate that this arrangement is dependent upon the degree of contraction of a particular proglottid, for it is possible to observe both conditions within a single strobila. (See Figs. 22-24). Moreover, variations in the size of individual testes throughout the given ranges occur among individual worms.

Variations in the prostate gland are common and are possibly associated with the degree of sexual maturity of a proglottid. (Figs. 25-27). In various specimens of Marsipometra hastata, it is possible to find segments within which the seminal receptacle appears to be absent. Closer examinations of whole mounts and of sectioned material indicate that the organ, although present, may be undeveloped.

Differences between Marsipometra hastata and M. confusa in the nature of the uterus are correlated with results obtained by excessive flattening or stretching of the worms. Distortions in the shapes of organs as a result of various techniques have been clearly illustrated by Ulmer (1950). Some of the changes described in that report resemble the conditions found in preparations of M. confusa. Distortions due to pressure become more apparent if worms are old or dead at the time of fixation.

The position of the vaginal opening into the genital atrium may also be highly variable. Within a single strobila, although this opening usually occurs anterior to that of the cirrus, it may lie posteriad in rare instances.

In view of the foregoing evidence, and after studying the wide variation characteristic of specimens of Marsipometra hastata, it becomes apparent that the distinctions between M. confusa and M. hastata are insignificant. Consequently, on the basis of priority, the specific designation M. hastata should be retained and that of M. confusa should be placed in synonymy with it. A redescription of the species, together with a complete synonymy follows, with additions to or modifications of previously published accounts indicated by underscoring.

Marsipometra hastata (Linton, 1898), Cooper, 1917

Dibothrium hastata Linton, 1898

Bothriotaenia hastata Ariola, 1900

Marsipometra hastata Cooper, 1917

Marsipometra confusa Simer, 1930 NEW SYNONYMY

Maximum length 243 mm., proglottids measuring up to 2.5 mm. x 2.0 mm., 1.0 mm. in thickness. Proliferation zone conspicuous, extensive in young worms; margins of proglottids serrate, often overlapping slightly. Muscles poorly to moderately developed. Scolex prominent, bothria distinct in live worms, often shallow and inconspicuous in dead specimens. Apical plate set off by circumferential markings, maximum width less than base of scolex. Testes 80 to 120 microns in diameter, arranged in single or multiple layers, number highly variable, ranging from 130 to

slightly over 200. Prostate gland large, well-developed in mature proglottid, medial to cirrus sac, extending from floor to roof of medulla. Seminal vesicle variable, in median end of cirrus sac. Vas deferens highly convoluted, dorsal and lateral to uterus. Genital atrium shallow to deep, at mid-lateral margin, alternating irregularly. Cirrus opening terminal, with vaginal opening ventral, primarily anterior, occasionally posterior. Seminal receptacle variable in shape, sharply set off from vagina. Ovary tubulolobular, reniform, located in posterior one-third of proglottid. Vitellaria in right and left dorsal and ventral fields, confluent laterally; in immature proglottids may be confluent anterior and posterior to uterus. Uterus sacculate, central, occasionally extending to anterior margin of proglottid. Uterine pore ventral, developing after uterus fills with eggs. See Figs. 15-21 for illustrations of typical specimens.

Eggs operculate.

Host: Polyodon spathula Walbaum.

Location within host: Anterior intestine and spiral valve.

Distribution: Common in Mississippi, Missouri, and Ohio River drainages. Collections have been reported from Ohio, Illinois, Iowa, Nebraska, South Dakota, North Dakota, Montana, Missouri, Mississippi, Tennessee, and Arkansas.

Distribution within the Host

Worms removed from freshly-killed fish are most abundant in that area of the intestine between the pyloric ceca and the spiral valve. Approxi-

mately 80% of the cestodes collected from live fish are localized in this anterior region of the intestine. The remaining 20% are distributed primarily in the spiral valve, but occasionally specimens may be found in the pyloric ceca. Worms from the anterior portion of the intestine are vigorous, active, and show no distortions. When removed from the body, they expand and contract, thrusting their scolices in many directions. Tapeworms from the spiral valve are the largest specimens encountered and carry a greater proportion of gravid proglottids than do worms from other areas. They are much less active and their behavior suggests that they are old worms. Specimens found in the pyloric ceca usually occur in knotted masses at the distal ends of the ceca, where they are heavily coated with mucus and are lemon-yellow in color. When removed and placed in normal saline solution, they appear greatly distorted. Such conditions may indicate that these are worms which have strayed from the more favorable areas found in the intestine.

Post-mortem examinations of paddlefish indicate that the cestodes may be found in large numbers in the pyloric ceca, stomach, esophagus, branchial chambers, or on the external surface of the body. Worms reach these areas by migrating soon after the death of the host and it is not unusual for them to appear at the normal body openings within one hour after the death of the host. Such migrating worms are often distorted and may show pronounced changes in the nature of their scolices and strobili. Cestodes remaining within the intestine of a dead fish exhibit few changes if removed within the first two hours after death. If left for a longer interval, the number of distorted specimens will increase

rapidly with time.

Immature worms exhibit a similar distribution to that of the adults. Very few of them are ever found in the pyloric ceca or in the spiral valve; the majority of them develop in the anterior region of the intestine. Large numbers occur in the crypt-like pouches lining the wall of this region of the digestive tract. Upon the death of the host, juvenile worms will migrate actively and in such cases are found in bizzare locations such as the gills or mouth cavity.

Marked seasonal fluctuations were noted in Marsipometra hastata collected from the Mississippi River in Pool 19 near Burlington, Iowa and from the Missouri River at the tailwaters of Fort Randall Dam at Pickstown, South Dakota. The heaviest concentrations of gravid worms occur during the months of April, May, and early June. During these months, the cestodes do not increase in length but show a marked increase in the number of gravid proglottids. After mid-June, gravid worms begin to decrease and by late July only a few adults or juveniles are found within a paddlefish. By mid-August the infections again begin to build up. Large numbers of juveniles can be found, some of them less than one millimeter in length. By late September the infections are again well established and mature, but not gravid, worms are common. The cestodes then grow rapidly and by mid-January are primarily mature adults containing many apparently gravid proglottids. The release of eggs, however, does not occur until late April when the water temperature reaches approximately 60°F.

It is interesting to note that old worms are those most likely to undergo distortions due to changes in environment. It is therefore understandable why worms collected in late winter and early spring show considerable morphological variation. The original description of Marsipometra parva was based on worms collected from late February to late April, that of M. confusa on worms collected from February to September (Beaver and Simer, 1940). It is interesting to note that M. parva and M. confusa were recovered at the time of year when distortions due to age or other factors are most prevalent. Pertinent data concerning the state of the hosts from which these species were collected are missing in Beaver and Simer's report.

Pathological Effects

The scolex of Marsipometra hastata is equipped with two shallow, saucer-like bothria, the margins of which are mobile and provide a weak adhesive force for attachment of the worm to the wall of the intestine. Wardle and McLeod (1952) suggested that worms possessing bothriate scolices use them as organs of locomotion rather than for permanent fixation. In this study, most worms had their scolices thrust into the crypt-like pits lining the intestine (Fig. 10) but readily released their hold under slight pressure. If the scolex has penetrated into the glands lining these pits, a connective tissue capsule is formed around it, effectively locking it in position (Fig. 11). Such cases, however, are exceptional. More commonly, there are less pronounced changes in the host tissue. In the immediate area of attachment, the

mucous membrane is damaged. Some epithelial cells are destroyed but the lamina propria and submucosa are unaffected. Accumulations of macrophages and eosinophils indicate a chronic inflammatory response to the cestodes. Heavy accumulations of mucus accompany the presence of the worms, but since the normal histology is unknown, the degree of change cannot be ascertained. A diffuse and less intense chronic inflammatory reaction to the tapeworms is suggested by the presence of macrophages and eosinophils throughout the mucosa of the intestine. Evaluations of this latter condition are difficult for several reasons. Studies on the normal histology of the paddlefish are lacking and it is difficult to obtain uninfected fish for comparison. Furthermore, the presence of cysts of juvenile ascarid nematodes in the tunica muscularis complicates the analysis of the host's response to the parasites. In the immediate area of the nematode cysts, permanent tissue alterations occur. A connective tissue capsule is formed and macrophages accumulate in these areas.

EGGS

Worms collected from January through March, 1958 possessed many gravid proglottids. Exposure of such segments to tap water, distilled water, or various natural waters failed to initiate egg-laying. To secure eggs, it was therefore necessary to dissect the worms. Beaver and Simer (1940), however, reported that Marsipometra hastata laid eggs freely when exposed to cold artesian water. Similar results were reported by Thomas (1929) for Haplobothrium globuliforme.

Dissection of the worms to remove eggs from the uteri yielded eggs of various sizes in differing stages of development. Those eggs examined during the months of January and February, however, showed little or no development. During the latter weeks of March, on the other hand, it was possible to observe early embryonation. By early April, hooks were visible within the larvae and the eggs were now shed readily.

Normal, well-developed eggs (Fig. 6), naturally released from the worm, are subspherical, thin-shelled, operculate, and filled with yolk material surrounding the embryo. They measure 57.2 (38-70) microns x 59.2 (40-73) microns (based upon measurements of 80 living, unflattened specimens). These dimensions compare favorably with those given by Beaver and Simer (1940). The shells of the eggs of Marsipometra hastata are very thin, hyaline, and devoid of color or external markings. They are easily broken by coverslip pressure and soon collapse after the escape of the enclosed coracidium. The thickness of the shell varies from one to three microns. Beaver and Simer (1940) in their emended

diagnosis of the family Amphicotylidae refer to the eggs as "... non-operculate with extremely thin shells...". My studies would indicate otherwise. Observations of hatching in a depression slide under 440 magnifications and examinations of the vacated shells show that the eggs rupture along a line approximately 21 microns from the opercular end, providng an opening approximately 24 microns in diameter. The line of separation is not a smooth suture as has been described for certain other pseudophyllideans. Instead, it forms a highly irregular line, quite unlike that indicated by Vogel (1930) for Diphyllobothrium latum. The operculum will be discussed further in a following section concerning hatching.

Since normal, well-embryonated eggs hatch immediately after contact with water at room temperatures, it was necessary to develop techniques to retard their hatching. Eggs laid in water at temperatures of 61°F. or less do not hatch. Two methods of storage were found suitable for such eggs. One involved continuous refrigeration, the other, the transfer from cold water to physiological saline solutions. Neither method has any apparent effect upon the viability of eggs. To initiate hatching, one need only to return them to warm water. Eggs of Diphyllobothrium latum, however, will hatch in either sea or fresh water (Redlich, 1925). St. Markowski (1935b), on the other hand, found definite requirements for the hatching of Bothriocephalus scorpii eggs. The eggs of this marine cestode will not hatch if placed into fresh water and the development of immature eggs is retarded.

If gravid uteri are removed from Marsipometra hastata in early winter, the eggs contained therein are very different from the normal eggs described above. They are spherical, highly variable in size (26-101.5 microns), and always show a wide, clear transparent peripheral area. The contents of such eggs appear granular and diffuse rather than cellular. Their shells appear thinner than those of mature eggs. By early April, well-developed normal eggs are naturally shed by the adult cestodes and these unusual eggs become less numerous. In late March, they are even less common. Whether these spherical, thin-shelled eggs are normal stages of development or abnormal eggs has not been determined. An interesting feature concerning such eggs is their reoccurrence in worms collected in late fall. In October and November, worms do not lay eggs readily and upon dissection of the uterus of an apparently gravid proglottid, one may observe large numbers of these peculiar eggs. Beaver and Simer (1940) discuss the occurrence of various types of eggs from worms in their collections, and although they illustrate them, do not discuss their significance.

As indicated above, embryonation of normal eggs becomes apparent in late March and egg laying then commences. Prior to this time, eggs are not released. Apparently, eggs removed from the uterus by dissection before late March are insufficiently developed and may undergo considerable distortion when exposed to water. Perhaps due to incomplete formation of the shell or of its associated membranes, the eggs may show an unusually pronounced swelling. None of these eggs were ever observed to

hatch. Their presence is apparently not the result of a lack of fertilization, since 95 per cent of the eggs normally laid are viable.

INCUBATION AND HATCHING OF EGGS

Beaver and Simer (1949) reported that adult cestodes of the genus Marsipometra released eggs readily when placed in artesian or rain water and that such eggs hatched almost immediately, liberating ciliated onchospheres. Thomas (1929) found that eggs of another primitive pseudophyllidean cestode, Haplobothrium globuliforme, hatch several minutes to one hour after entering the water. During the course of my investigations, worms collected on January 18, 1958 were exposed to various types of water, including artesian water. Not only did the worms fail to lay eggs, but when eggs were removed by dissection of the uteri of gravid proglottids, hatching did not occur. Since a great variation in the times required for incubation is recorded in the literature, numerous cultures of eggs were prepared for incubation. Ekbaum (1937) had observed the incubation period of Triaenophorus crassus to vary from three hours to eight days. The experiments herein reported involved the removal of eggs from the uteri by dissection and placing them into small stender dishes filled with various types of water. These included unchlorinated tap water, distilled water, water from a farm pond, farm tile water, and artesian well water. Eggs were incubated under normal daylight conditions at room temperature (72°F.). During the first hour of incubation, observations were made every ten minutes in case hatching might occur within a short time. Hourly observations were then made during the first 16 hours. Thereafter, cultures were examined every morning and evening. Water was changed daily and the eggs were

studied under a dissecting microscope (9X - 54X) to detect any changes in development or to see if hatching had occurred. No such changes were observed. Numerous ciliates and rotifers developed in the water from the farm tile and farm pond. Six days after beginning incubation, mold appeared in all cultures except in the one containing distilled water. Addition of one drop of concentrated formalin to each contaminated culture retarded the growth of the mold but did not affect the protozoans or rotifers. After ten days of incubation, eggs in all cultures began to disintegrate and by the 19th day all eggs were in such poor condition that the experiment was terminated.

Worms from a second collection, taken on February 9, 1958, failed to shed eggs when exposed to the various types of water. Again, dissection was necessary in order to secure eggs. No hatching was observed when they were exposed to water. Vergeer (1936) reported that by increasing the temperature it was possible to reduce the time required for incubation of eggs of Diphyllobothrium latum. Consequently, constant temperature cabinets were obtained for use in incubating the eggs. Five cultures were prepared from each of the types of water used previously, in addition to another culture containing water collected from the Mississippi River in the area from which the cestodes had been taken. One culture of each type of water was then incubated at room temperature (72°F.) under daylight conditions. The remaining cultures were placed in unlighted constant temperature cabinets and incubated at temperatures of 72°, 79°, 90°, and 98.6°F., respectively.

After three days, all natural water cultures were again heavily

populated with ciliates and rotifers. These became so abundant that it would have been difficult to distinguish any coracidia which might have emerged. Essex (1927a) reported that eggs of Diphyllobothrium latum treated with formol did not hatch. Mattes, however, had used various acids to vary the pH levels in hatching experiments on eggs of Fasciola hepatica with no harmful effects. Consequently, two drops of phenol were added to each culture to remove the invertebrates. After ten days incubation in darkness at the elevated temperatures, or in daylight at room temperature, eggs were again in various stages of degeneration and the experiment was halted on the 14th day. Up to this time, no change in the development of the eggs had been noted.

Vogel (1929) found that eggs of Diphyllobothrium latum did not hatch if incubated in darkness, but Li (1929) found that eggs of Diphyllobothrium decipiens and Diphyllobothrium erinacei hatched equally well under conditions of light or darkness. It is known that light has a stimulatory effect on hatching for many species (Van Haitsma, 1931; Smyth, 1955; Mueller, 1959). Mattes (1926) in his studies on the hatching of eggs of the trematode, Fasciola hepatica, found that varying the pH often induces hatching.

Prior to the next attempt at hatching, new samples of the above mentioned types of water were collected. Determinations of pH indicated the following values for the various types of water:

Farm tile	5.5	Tap water	7.0
Farm pond	6.5	Dist. water	7.0
Miss. River	7.0	Artesian water . . .	7.5

These values fall within the ranges found acceptable for eggs of

Fasciola hepatica as determined by Mattes (1926).

A third collection of worms was made on April 4, 1958. These worms readily laid eggs, most of which were in advanced stages of embryonation. About 30% of the eggs were observed to contain embryonic hooks when examined under oil immersion. Cultures were prepared and incubated as before. Again, no hatching occurred. Attempts to stimulate hatching by exposing the eggs to bright light met with no success. Fourteen days after its initiation, this experiment was terminated, again due to deterioration of the eggs.

On April 26, 1958, a fourth collection of tapeworms was made. Worms exposed to cold river water immediately after their removal from the host, released eggs in great numbers. However, no hatching was observed. Worms removed from living fish were placed in solutions of normal saline and refrigerated while being transported to the laboratory. At the laboratory, worms transferred to warm river water laid eggs in profusion and hatching commenced at once. Within minutes, about 95% of the eggs laid had hatched and coracidia were observed actively swimming about. Similar results were obtained with every type of water used in previous experiments, including those solutions to which weak formalin or phenol had been added, under all of the conditions utilized previously with the exception of the 98.6°F. incubation. The cabinet maintained at this temperature was no longer available and the incubation was therefore not repeated. Worms placed into cold river water laid eggs readily but these eggs did not hatch until the water was warmed to 63 F (± 2°). Worms transported and maintained in refrigerated saline did not lay eggs.

However, when these same worms were transferred to water other than saline, eggs were released and hatching was almost immediate. Eggs transferred from cold water to saline did not hatch even when the temperature of the latter rose past 63°. These same eggs hatched readily when transferred back to warm fresh water.

These results appear to indicate that failure of eggs to hatch in the first three attempts was not associated with pH, light, incubation period, or contamination. Rather, it would seem that, in nature, hatching is associated primarily with the degree of maturation of the embryo, and apparently is secondarily related to the temperature of the river water. In the laboratory, although saline inhibits egg laying and retards hatching, it does not affect the viability of the eggs. Contact with fresh water seems to serve only as a stimulus to initiate the emergence of adequately developed embryos. In their experimental attempts to hatch the eggs of blood flukes, Onorato and Stunkard (1931) found that the operculate shells did not open until the enclosed miracidium was mature, regardless of the medium into which the eggs were placed. See Table 1 for a summary of the hatching experiments conducted on eggs of Marsipometra hastata.

An opportunity to check the validity of the above conclusions presented itself during the early summer studies at Fort Randall Dam on the Missouri River near Pickstown, South Dakota. When the first collection from that area was made on June 14, 1958, temperatures in the current were 53°F., whereas those in backwater areas averaged 59°. Worms from this collection, when placed into warm lake water, laid eggs

Table 1. Summary of hatching experiments (January - April, 1958)

Type of water:	Miss. River	Farm pond	Farm tile	Artesian well	Distilled water	Tap water	River Temp.(F.)	
pH:	7.0	6.5	5.5	7.5	7.0	7.0	Current	Backwaters
Exp. No. 1 (Jan. 19, 1958) Daylight 72°F.		-[a]	-	-	-	-	32	32
Exp. No. 2 (Feb. 9, 1958)							32	32
Daylight 72°F.	-	-	-	-	-	-		
Darkness 72°F.	-	-	-	-	-	-		
Darkness 79°F.	-	-	-	-	-	-		
Darkness 90°F.	-	-	-	-	-	-		
Darkness 98.6°F.	-	-	-	-	-	-		
Exp. No. 3 (April 4, 1958)							49	56
Daylight 72°F.	-	-	-	-	-	-		
Darkness 72°F.	-	-	-	-	-	-		
Darkness 79°F.	-	-	-	-	-	-		
Darkness 90°F.	-	-	-	-	-	-		
Darkness 98.6°F.	-	-	-	-	-	-		
Exp. No. 4 (April 27, 1958)							57	66
Daylight 38°F.	-	-	-	-	-	-		
Darkness 38°F.	-	-	-	-	-	-		
Daylight 72°F.	*[b]	*	*	*	*	*		
Darkness 72°F.	*	*	*	*	*	*		
Darkness 79°F.	*	*	*	*	*	*		
Darkness 90°F.	*	*	*	*	*	*		

[a](-) indicates negative results
[b](*) indicates positive results

readily, but hatching success was less than 0.01%. A subsequent collection from that area was made on July 5, 1958. Water temperatures then ranged from 60°F. to 65°F. Worms now laid eggs freely in the laboratory and hatching success approached the 90% level. It becomes apparent then, that temperature is a major factor in the development and hatching of fully embryonated eggs.

In my studies, the first successful hatching of the eggs of Marsipometra hastata was observed on April 27, 1958. Previously, worms collected on April 4 contained embryonated eggs and although six-hooked onchospheres were visible within the shell, none of those eggs hatched. On April 27, however, coracidia emerged in great numbers. The eggs rupture along a line approximately 21 microns from the operculate end, providing an opening approximately 24 microns in diameter. Emergence from the egg is so sudden and abrupt that eggs seem literally to explode. A similar phenomenon occurs in the hatching of the eggs of Bothriocephalus scorpii (St. Markowski, 1935a). Among most pseudophyllidean cestodes, however, hatching is more commonly a less abrupt process. Due to the suddenness of hatching of M. hastata eggs, observations were somewhat limited. Immediately prior to its emergence, the coracidium becomes restless and its cilia beat vigorously. Ekbaum (1937) reports similar behavior for the coracidia of Triaenophorus crassus just before hatching. Granular material between the shell and the larva is very evident and moves freely as the cilia beat. None of the droplets reported by Mueller (1935) could be observed between the shell and the coracidium. Soon after the larva becomes active, the

operculum opens due to some unexplained stimulus and the ciracidium is expelled.

Various theories have been proposed to explain the nature of the hatching phenomenon in helminth eggs. A. P. Thomas (1883) described the hatching of the eggs of Fasciola hepatica as "... a vigorous extension of the body (of the miracidium) causes the operculum to fly open ...". E. L. Taylor (1926) observed a hexacanth embryo of Davainea cesticillus (Cyclophyllidea) "tear its way through the inner membranes and shell" but he speculated that this would not be the case for species in which the onchosphere was contained in a ciliated embryophore. Vogel (1929) found that eggs incubated in lakes at great depths would hatch when transferred to shallow water. Hatching, he claimed, was therefore due to a change in the pressure balances within and without the egg. None of my observations support the above contentions. Instead, some force acting outside the coracidium seems responsible for the sudden rupture of the eggs. Mattes (1926) described a protoplasmic cushion between the coracidium and the shell of the egg. According to his observations, the expansion of this cushion, caused by an unknown stimulus, was responsible for forcing the operculum to open. Onorato and Stunkard (1931) have shown that the release of the operculum is not merely a matter of physical pressure. In their experiments on the eggs of blood flukes, the operculum failed to open, regardless of the medium into which the eggs were placed, unless the enclosed larva was mature. They, therefore, suggested the presence of a hatching enzyme produced by the mature miracidium. Hatching, according to their findings, was

the combined result of a loosened operculum and a hypertonicity of the egg contents. The escape of the miracidium was initiated by the influx of water and completed by movement of its cilia. In a single instance, I observed that the operculum did not separate abruptly from the remainder of the shell. Instead, it slowly slid off at an oblique angle. The enclosed coracidium emerged slowly, its cilia beat feebly, and the larva expired minutes after its release. An objection to the theory of hypertonicity arises from the work of Redlich (1925) who showed that the eggs of Diphyllobothrium latum will hatch equally well in sea or fresh water. In salt water, the osmotic imbalance would be greatly reduced, perhaps enough so as to eliminate the expulsive force due to the influx of fluid. Other studies indicate that additional factors may also influence the hatching of mature eggs. Van Haitsma (1931) was a proponent of the idea that light stimulated the release of a hatching enzyme. More recently, Rowan (1956) accepted the results of Onorato and Stunkard but also found that light had a stimulatory effect on hatching. He postulated that light is perhaps the stimulatory agent causing the miracidium to release the enzyme which digests away the cementing substance around the operculum. His results indicate that the hypertonicity of the egg contents forces the miracidium out of the opened shell and that muscle activity on the part of the larva is only secondary. My studies would indicate that perhaps temperature is a more important factor than light in the initiation of the hatching process. In my attempts to hatch the eggs of Marsipometra hastata, a critical temperature of 61°F. was required before hatching would begin.

At temperatures above 61°F., eggs hatched regardless of light conditions and hatched equally well in complete darkness. Similar results had been recorded much earlier by Li (1929) in his studies on the genus Diphyllobothrium. That refrigeration is a very effective method of preventing hatching has been shown in my studies and those of Li (1929) and Mueller (1959). In his attempts to culture Spirometra mansonoides on artificial media, Mueller has shown that light will stimulate some eggs to hatch, but has also found that eggs exposed to light refuse to hatch if under refrigeration.

CORACIDIA

After their release from the eggs, coracidia of Marsipometra hastata (Fig. 7) pause momentarily, swell slightly, and then begin to move actively about with a constant, gentle rolling motion. They swim in a spiral along straight lines, but continually change direction, all the while rotating about the axis of their line of travel.

Apparently the longevity of coracidia varies among individual species of cestodes. The literature contains many records of the life spans of coracidia. In the table below are some of the more pertinent data.

Table 2. Life span of coracidia

Worker	Species	Longevity in water	Temperature
Li (1929)	D. decipiens	2 days	not indicated
Li (1929)	D. erinacei	2 days	not indicated
Thomas (1929)	H. globuliforme	1 day	
		1 month in saline	not indicated
St. Markowski (1935)	B. scorpii	2-3 days	68-72°F.
Vergeer (1935)	D. latum	2 days	70°F.
		7-9 days	48-52°F.
Ekbaum (1937)	T. crassus	3-4 days	not indicated
Meyer (present study)	M. hastata	9-10 hours	72°F.
		3-4 days	61°F.
		10 days	40°F.

At the end of one hour in water at room temperature (72°F.), coracidia of Marsipometra hastata are still actively swimming but pause frequently and sink to the bottom where they lie motionless for short periods of time. At irregular intervals they resume their characteristic rolling movement. This type of behavior persists for approximately three more hours after which the majority of coracidia become quiescent, sink to the bottom, and

lose their cilia. The ciliated embryophores may be found in the container at that time. After another 4½ hours in water at room temperature, many of the onchospheres die and begin to disintegrate. The life span of coracidia is much longer, however, in cooler water. When kept in water at 61°F., coracidia show less activity but are much longer lived. If refrigerated within one half hour after hatching, it is possible to maintain them in an inactive state for several days. During the cooling treatment, the larvae become quiescent but will resume their activity whenever the water is warmed above approximately 55°F. If warmed and then recooled, the coracidia first become active as the water warms, then sink to the bottom and lie motionless as the water cools. This phenomenon may be repeated several times with no apparent effect on the onchospheres.

Seventy-nine living coracidia, measured under high-dry magnification (430X) with no cover glass pressure average 58.5 microns in diameter. Cilia measuring 15 microns in length cover the entire body whose surface is characterized by numerous swollen areas. (Figs. 8 and 14). Vogel (1929) reported that the coracidia of Diphyllobothrium latum possess much longer cilia at the anterior pole than over the rest of the body. No such differentiation of cilia could be observed in any of my specimens. The onchosphere itself has a mean diameter of 43.4 microns and contains six hooks situated in a distinct zone near the posterior end of the embryo. These hooks have a mean length of 13.7 microns and have a characteristic shape (Fig. 2).

In the area between the onchosphere and the embryophore are many

transluscent granules. The exact nature of these granules is not certain. Li (1929) observed similar structures in the coracidia of Diphyllobothrium decipiens and Diphyllobothrium erinacei which were described as excretory granules.

The body of the onchosphere itself is filled with cells of varying sizes with an aggregation of larger cells at the pole opposite the hooks. Preparations with Delafield's hematoxylin or Heidenhain's iron hematoxylin and counterstained with eosin have shed little light on the nature of these cells. Ogren (1959) described prominent epidermal glands "behind the hooks" in onchospheres of Dilepis undula (Cyclophyllidea). Vogel (1929) described strange cells in the onchospheres of Diphyllobothrium latum which stained with azure-eosin or methylgreenpyronin. These he called germ cells. The cells I have observed in the onchospheres of Marsipometra hastata more closely resemble those described by Vogel but detailed studies on their nature have not been carried on.

A single pair of flame cells, just anterior to the embryonic hooks, may be readily seen in living specimens (Fig. 1). The use of Nile blue sulphate and neutral red proved useful in viewing these structures. Although the beginnings of excretory tubules are visible, it has been impossible to trace them in their entirety. In all cases, however, the visible portions of the tubules lead toward the zone bearing the embryonic hooks.

INTERMEDIATE HOSTS

In an attempt to determine the intermediate host or hosts involved in the life cycle of Marsipometra hastata, several types of investigations were undertaken. A thorough study of the food habits of the paddlefish provided certain useful clues to the invertebrates which might serve as hosts. By comparing the stomach contents of paddlefish from two completely independent areas in which the cestodes are endemic, it was possible to eliminate certain organisms as potential hosts. Finally, experiments were conducted in which the coracidia were fed to a variety of invertebrates in the hope of obtaining subsequent developmental stages.

The diet of 88 Polyodon spathula collected from the Mississippi River near Burlington, Iowa consisted primarily of animal matter. Much of the bulk of the stomach contents consisted of mayfly naiads of the genera Hexagenia and Pentagenia. Other insects occurred occasionally but were not abundant. Zooplankters were the most abundant organisms and included species of Daphnia, Leptodora, Bosmina, Cyclops, and Diaptomus. Very infrequently, large quantities of diatoms, desmids, and filamentous algae were present. A partially digested fish, probably a river darter, Percina shumardi, was found in the stomach of one paddlefish. Similar food studies were carried out on 27 Polyodon taken from the Missouri River at the tailwaters of Fort Randall Dam, Pickstown, South Dakota. Fish from this area had fed almost exclusively on plankton. Zooplankton formed approximately 85 per cent of the diet,

both in total numbers and in total volume. Phytoplankton, primarily Asterionella, formed most of the remainder. On rare occasions, a few dragonfly naiads were found. A comparison of the sets of data from the two areas helped eliminate the consideration of several organisms as possible hosts. Only Daphnia, Bosmina, Cyclops, and Diaptomus were common to both areas. Leptodora kindti is so uncommon that it scarcely seems likely that it might serve as an intermediate host. Members of the genus Bosmina are too small to be able to ingest the coracidia so they may be disregarded on the basis of size. Insect larvae are unknown as intermediate hosts for pseudophyllidean cestodes. However, because of the abundance of such larvae in the stomachs of the fish collected in the Mississippi River, it was considered advisable that they be included in any experimental feeding of coracidia. Amphipods are known to serve as intermediate hosts for the primitive cestode, Cyathocephalus truncatus, (Wisniewski, 1933) and these too, were included in the experimental studies discussed below.

Before beginning studies on the life cycle of Marsipometra hastata, laboratory-reared cultures of possible arthropod hosts were secured from a scientific supply house. Other specimens were collected from local bodies of water. Stone-fly, hellgrammite, and caddis fly larvae were collected from the Des Moines River near Boone, Iowa and placed in well-aerated aquaria. The stone-flies failed to survive but hellgrammite and caddis fly larvae could be maintained with little difficulty. Hyalella species were collected from Lake West Okoboji, Iowa near Iowa Lakeside Laboratory, Milford, Iowa. Daphnia pulex Forbes, Ceriodaphnia

reticulata (Jurine), Hyalella azteca (Saussure), and Cyclops bicuspidatus Claus were secured from the Carolina Supply Company. These crustaceans were maintained in well-aerated aquaria containing strands of Elodea and Myriophyllum. For the first week, all microcrustaceans were fed a yeast emulsion as recommended by Needham, et al. (1937). Several days later an algal culture (Ankistrodesmus falcatus) was added to each aquarium. Growth of the crustaceans was only fair and dense populations failed to develop when yeast and algae were included in the diet. Hyalella azteca was fed on a diet of pellets normally designated as pigeon food. In addition, lettuce was added daily. Not only did the Hyalella respond well to this diet but microcrustaceans in the same aquarium showed great increases in number. An unidentified ostracod in the same aquarium also favored this diet. Consequently, all species of zooplankters were gradually shifted to a diet of pigeon pellets and lettuce. Populations of Cyclops, Daphnia, and Ceriodaphnia reached high concentrations but were prone to be cyclical in nature. Peak populations occurred approximately every 24 days.

With large numbers of crustaceans available for experimental work, preliminary feeding experiments were undertaken on May 25, 1958. At that time, laboratory-reared cultures of Hyalella azteca, Daphnia pulex, Ceriodaphnia reticulata, Cyclops bicuspidatus, and an unidentified species of ostracod were exposed to coracidia. Using two-inch stender dishes as aquaria, two sets of 12 specimens of each species were prepared. In each experiment, coracidia were added. After allowing the microcrustaceans to feed, the water was removed and replaced, thereby

removing uningested coracidia. In the initial experiment, approximately 1000 coracidia were left in the containers for 15 minutes. At the end of that time, one set of each crustacean species was examined by dissection. All were found to have fed actively. The remaining set was observed hourly under a dissecting microscope (9X - 54X) to detect any migration by the cestode larvae. Within six hours, hexacanth embryos appeared in the haemocoels of Daphnia and Hyalella. Ten hours post-exposure, these species exhibited signs of distress and paralysis of the limbs. Within the next two hours, all of the Hyalella had died. The condition of the Daphnia continued to deteriorate and 36 hours after exposure, all had expired. Post-mortem studies on these species showed that their haemocoels contained numerous onchospheres. Cyclops, Ceriodaphnia, and the ostracod species were uninfected. It was noted that Daphnia and Hyalella were much more efficient in capturing and ingesting coracidia than were any of the other organisms. These two species were gorged with cestode larvae. Because of the high mortality of Daphnia and Hyalella in these preliminary experiments, it was suspected that an excessively high number of coracidia had been used. Death of invertebrate hosts due to the penetration of large numbers of onchospheres has been noted by Thomas (1937) in his studies on Bothriocephalus rarus.

Subsequent experiments on the larvae of Marsipometra hastata utilized varying numbers of coracidia and differing periods of exposure. An experiment using the same species of animals but involving only 200 coracidia in a 15 minute feeding interval produced negative results in all species.

Exposure of hellgrammite and caddis fly larvae to thousands of coracidia for one hour also produced negative results. During late June, Diaptomus oregonensis Lilljeborg, D. pallidus Herrick, D. silicoides Lilljeborg, Cyclops fimbriatus Fisher, C. fluviatilis Herrick, and C. insignia Claus were collected from the Missouri River and from Lake West Okoboji, Iowa. Identifications were made using Pennak (1953), McDonald (1939), and Stromsten (1920a). All specimens of crustaceans used were examined individually under a dissecting microscope (54X) using transmitted light to detect the presence of any foreign bodies within their haemocoels. By refrigerating the copepods to 38°F. it was possible to inactivate them long enough for close inspection without injuring them. Numbers of these zooplankters were exposed to 200 coracidia for 15 minutes. Of all the microcrustaceans exposed, only Diaptomus oregonensis became infected. Thirty per cent of those exposed later exhibited cestode larvae within their haemocoel. The remaining species were negative. Eight hours after exposure, onchospheres were visible within the haemocoel of D. oregonensis, but 40 hours later no trace of the onchospheres or of their embryonic hook could be found. Daily mortality was high in Diaptomus cultures and examination of dead infected specimens revealed the presence of peculiar irregularly shaped, light-brown masses in the anterior cephalothoracic regions of the haemocoel. Control specimens did not show these bodies. Since these masses bore no resemblance to the typical procercoid larvae known to occur among other pseudophyllideans, little significance was given to their presence.

A similar experiment was conducted, this time with an additional

culture of Cyclops bicuspidatus, a species which had previously been negative. Thousands of coracidia were used and the copepods were allowed to gorge themselves. In many, the digestive tract was tightly packed with cestode larvae. That many onchospheres were digested or killed was indicated by the recovery of fragments which had passed through the digestive tract. In others, onchospheres which had shed the embryophore had passed through the gut, apparently unscathed. Such onchospheres could be found moving about in an amoeboid fashion on the bottom of the container. Eight hours later, onchospheres were observed in the haemocoels of Diaptomus oregonensis and C. bicuspidatus. In previous experiments, however, the latter species had been refractile to infection. The feeding habits of this species may explain this discrepancy in results. Except when feeding rapidly, C. bicuspidatus injures many of the coracidia and enclosed onchospheres. Furthermore, passage of food through the gut is fairly rapid if the quantity of food is limited. It is possible that in previous experiments the onchospheres might have been digested or expelled before they were able to penetrate the wall of the gut. Such cases have been reported by Mueller (1959b) in his studies on Spirometra mansonoides. Li (1929) found great variability in the susceptibility of Cyclops affinis to larvae of Diphyllobothrium decipiens and Diphyllobothrium erinacei, even when the digestive tract of the copepod was tightly packed with coracidia. Essex (1927a) showed that although Diaptomus oregonensis is the probable host for Diphyllobothrium latum, varying degrees of susceptibility are shown by several other species. It is also probable that in my previous

experiments coracidia ingested by Cyclops bicuspidatus were insufficient in number to result in infection. The use of massive numbers of coracidia was recommended by Mueller (1959b) who felt that the copepods do not actively pursue the coracidia, but that infections are acquired as the result of chance collisions between the cestode larvae and the copepods. By increasing the number of coracidia, it is therefore possible to enhance the possibility of obtaining infected copepods.

Forty-eight hours after exposure, no trace of cestode larvae remained and within a week all infected copepods had died. The large numbers of coracidia used may have proved fatal to the hosts. Examinations of the dead crustaceans showed the presence of the peculiar irregular masses noted above. Since they were not found in control cultures and had appeared a second time under experimental conditions, the possibility that they might be developing cestode larvae was considered. As before, however, they bore no resemblance to previously described procercoid stages. At this time, attempts to maintain copepod cultures failed and experiments were terminated. Temperatures in the laboratory (often in excess of 80°F.) probably exceeded the maximal thermal tolerance of the copepods. Attempts to secure viable eggs in early fall were unsuccessful and further work was postponed until the summer of 1959.

DEVELOPMENT OF PLEROCERCOIDS

Experimental work during the summer of 1959 dealt primarily with Cyclops bicuspidatus and Diaptomus oregonensis. Cultures were prepared in late June preparatory to collection of gravid tapeworms. At that time, several aquaria containing copepods were accidentally left in a refrigerator during a weekend. It was later noted that the survival of refrigerated zooplankters was nearly double that of unrefrigerated ones.

Exposures of copepods to coracidia were made on June 25, 1959. Thousands of coracidia were again used but the period of feeding was reduced to five minutes. Both species of copepods fed heavily.

Following exposure, the infected copepods were returned to culture media and placed in the refrigerator (42°F.). Onchospheres were noted within the haemocoels of the arthropods eight hours later. Soon after their arrival in the haemocoel, the onchospheres began to change. In one copepod examined 32 hours after having ingested coracidia, a single hooklet was observed lying apparently free along the lateral margin of the onchosphere. Forty-eight hours after exposure, no trace could be found of the embryonic hooks and it was difficult to identify the onchospheres. Daily mortality of the Cyclops was low, but after four days the Diaptomus began to fail. As in the preceding year, the latter species did not respond to culture techniques. Cyclops, on the other hand, thrived and specimens were maintained for extended periods.

Four days post-exposure, the irregular masses were again evident

and it was observed that individual copepods harboring many of these bodies showed symptoms of distress and expired. Similar kills had been noted by Thomas (1937). Those zooplankters carrying only a few of these bodies appeared to show no ill effects. Continued observance of these bodies over the next 20 days indicated that they gradually increased in length. The irregular form disappeared and they gradually assumed the normal shape of a pseudophyllidean procercoid. It must be noted, however, that at no time was a cercomer observed, and had it not been for continued observation over a three-week interval, the larvae would have gone unrecognized.

Newly emerged coracidia, as noted above, measure 58.5 microns (average of 80 specimens) in diameter. Onchospheres which have recently entered the haemocoel measure 43.4 microns (average of 21 specimens) and move sluggishly in an amoeboid manner. Once within the haemocoel, their activity becomes greatly reduced. Occasional expansions and contractions occur during the first few hours but soon cease. The change in form from a regularly-shaped sphere to a berry-like mass occurs within a period of several hours (Fig. 4). Accompanying this change is an increase in size. By the end of four days the larva measures 77 x 65 microns (average of 14 specimens) and by the end of ten days, it measures 148 x 126 microns (average of 17 larvae). By the tenth day, no distinct internal structures are evident, no cercomer has formed, and no hooks can be found. The larvae are exceedingly fragile and are easily broken by cover-slip pressure. Most of the body consists of fairly large cells which appear highly granular. Large translucent granules are also

prominent. By the 14th day post-exposure, the body has elongated considerably. The diameter of the larva at this time does not increase but a considerable lengthening occurs. The surface of the body is smooth, and the larva has now assumed a sausage shape. At this stage, the larvae measure approximately 250 x 120 microns (average of 12 worms). They expand and contract at periodic intervals and from day to day may be found in various locations in the haemocoel of their host. Most often they occur in the regions of the cephalothorax, but it is not uncommon to find them well back in the abdomen where they may obstruct the passage of food through the digestive tract (Fig. 5). Little change in shape occurs after the 21st day but larvae continue to increase in size. The larvae develop a prominent and bluntly pointed anterior end. At 55 days they measure 0.511 mm. in length and 0.162 mm. in width (average of six specimens). Concentrations of nuclei suggest the beginning of a rudimentary scolex. No trace of the excretory system can be observed in living or preserved specimens. The larvae assume a lighter color which varies from light-brown to a nearly opaque white. As the age of the individual increases, the whiteness becomes more and more pronounced. No infected copepods lived beyond the 55th day post-infection and developmental stages of the cestode beyond that period are not available.

Suitable definitive hosts for continuing the study were unavailable. No one has yet succeeded in maintaining paddlefish in the laboratory for any length of time. Attempts by various workers to rear paddlefish from eggs have met with no success. For this reason, further studies on the life cycle were not feasible.

Many problems relative to host-parasite relationships remain unanswered. It is interesting that in one experiment, as noted above, Cyclops bicuspidatus appeared to be resistant to infection. However, in a later experiment, this host harbored the parasite in limited numbers. The experiments conducted in 1958 involved only large adult specimens. Possibly, an age immunity exists. Also, the numbers of coracidia used in attempted exposures and the nature of feeding habits of the intermediate host have already been noted as factors possibly affecting the infectivity of Cyclops.

The most striking feature in the early developmental stages of Marsipometra hastata is its failure to produce a typical procercoid larva. Nevertheless, several other species of pseudophyllidean tapeworms are known in which a cercomer is never formed. Such developmental stages were noted by Kuczkowski (1925) in his studies on Ichthyotaenia but he felt that they were "cast-off bladders" or cercomers of mature procercoids. Members of the genus Corallobothrium may develop certain forms which are devoid of hooks or cercomers (Essex, 1927b). Essex considered the proposal of Kuczkowski and while he felt it might be possible, could not explain why some of these bodies should have been larger than any well-developed cercomer. Haplobothrium globuliforme may produce forms either with or without a cercomer (Thomas, 1929). Thomas considered those larvae lacking a cercomer as retarded individuals which resulted from heavy infections in the copepods. Li (1929) observed larvae without a cercomer in Diphyllobothrium decipiens and D. erinacei but suggested that these might have resulted from injury by its Cyclops

host during ingestion.

A structure resembling a slight invagination at the anterior end of the larvae of Marsipometra hastata is visible in certain stages of its late development but it is never well formed. The oldest larvae observed within the copepods lack such a structure and have a bluntly pointed anterior apex. See Fig. 3.

Careful examinations of the intestines of infected definitive hosts were undertaken in an attempt to recover early developmental stages. Many small plerocercoids (Figs. 12 and 13), some of them less than 0.6 mm. in length, were found on two occasions in late August in crypt-like pouches which line the intestinal wall of paddlefish. Bothria were undeveloped in these specimens. Measurements of several of these specimens varied between 0.5 and 0.6 mm. in length and they were roughly diamond-shaped. Concentrations of nuclei clearly indicated the developing scolex and bothria, even though these structures were as yet incomplete. A comparison between the 55 day larvae observed in the copepod and the smallest ones taken from the intestine of Polyodon shows that the major difference is one of size. No specialization is apparent in the very young specimens recovered from the paddlefish.

Apparently, Marsipometra hastata does not require a second intermediate host in its life history. The larval form found in copepods probably represents a combined procercoid-plerocercoid stage. Such larvae have been described by Rosen (1918) for Abothrium infundibuliforme, a species which likewise does not require a second intermediate host. Complete studies on the food of Polyodon as discussed below

suggest little which would indicate the likelihood of a second intermediate host in the life cycle of Marsipometra hastata.

PART II. THE BIOLOGY OF *POLYODON SPATHULA* (WALBAUM, 1792) RAFINESQUE, 1820

REVIEW OF LITERATURE

The unusual shape of the paddlefish, Polyodon spathula (Walbaum) (Fig. 28), has aroused considerable interest in this fish since it was first described in 1792. Walbaum (1792) originally considered the paddlefish an aberrant shark and, under the name of Squalus spathula, included it among the chondrichthyean fishes. Rafinesque described it as Proceros spathula, calling it "a singular new genus of sharks", but later changed the generic designation to Polyodon when he (1820) described the fishes of the Ohio River. In this paper, Rafinesque listed the following synonyms for Polyodon spathula: Squalus spathula Walbaum, Polyodon feuille Lacepede, Polyodon folium Lacepede, and Planirostra edentula Rafinesque. Jordan and Evermann (1896) recorded as additional synonyms, Proceros maculatus Rafinesque, Planirostra spathula Owen, and Platirostra edentula Le Sueur. Although early workers considered the paddlefish to be a shark, subsequent workers have indicated that it is a remnant of an ancient group of primitive fishes which may once have been widespread. A review of fossil paddlefish was provided by Dean (1895).

At present, only two members of the Polyodontidae have survived; Polyodon spathula of the Mississippi River in the United States, and, according to Hussakop (1910), Psephurus gladius of the Yangtze River in China. Published data on the Chinese species are unavailable. A wealth of literature on P. spathula, however, has accumulated in the United States. According to D. H. Thompson (personal communication,

1958), large scale attempts to find the young of Polyodon were common in the late 1800's when workers were spurred on by the standing offer of a $1000 reward for the discovery of a specimen less than two inches in length. Many well-organized searches were conducted at that time, some with considerable financial backing, but all failed. Stockard (1907), with the aid of the Dyckman Fund of Columbia University, spent considerable time in 1904 and 1905 on the lower Mississippi River studying the behavior of the species. Although he failed to collect any young fish or naturally spawned eggs, he recorded many observations on the morphology and migrations of the adult fish. C. H. Danforth (1911) collected a number of small paddlefish from the Mississippi River near St. Louis, Missouri, on July 12, 1910. Publication of his data stimulated Barbour (1911) to describe a number of small specimens in the collection of the Museum of Comparative Zoology of Harvard University. The smallest specimen in that collection measured 35 mm., but data are lacking beyond the knowledge that it was collected in Arkansas by a Mr. G. Stolley, sometime prior to 1860. When the collection of Louis Agassiz was presented to Harvard University, a number of small Polyodon were found to be included. These had been taken by a Dr. Eastman in September, 1854, from the Mississippi River near St. Louis (Barbour, 1911). The above records represent the sum total of successful collections until May 14, 1932 when Dr. D. H. Thompson (1933) and his colleagues collected several 17 to 21 mm. post-larval paddlefish from a sandbar in the Mississippi River several miles below the town of Grand Tower, Illinois. Thompson and his co-workers made another

successful effort in the Mississippi River during May, 1944, near Cape Girardeau, Missouri. Although many collections of small paddlefish have been made since Thompson's catches, no one else has taken a fish smaller than two and a half inches in length.

Collections from Iowa lakes or from waters adjacent to Iowa contain small fish measuring from two and a half to 12 inches. The smallest were taken by W. W. Aitken (personal communication, 1958) in July, 1936 and measure from two and a half to three and a half inches.

R. M. Bailey, B. F. Stiles, and E. B. Speaker have also made collections of paddlefish but the smallest in any of these collections is four inches long. A preserved specimen measuring 4.1 inches was found in a collection of fish at the Iowa Lakeside Laboratory in 1958 but vital data are lacking.

During the late 1800's, an extensive fishery for paddlefish developed on the Mississippi River. In some instances, fishermen were reported to have used seines two miles long and 30 feet deep. A gill net, one mile in length, yielded 133 fish in one hour while set in a bayou in Washington County, Mississippi on May 16, 1905 (Stockard, 1907). There was little demand for Polyodon as a market fish until the supply of lake sturgeon for the eastern markets began to decline. Paddlefish meat was then dried or smoked and sold as sturgeon. Even more valuable than the meat was the caviar which could be made from the eggs. During periods when the fish were actively migrating, commercial fishermen took great numbers of gravid females. Stockard (1907) reported that a single fisherman was able to ship as many as 75 kegs of caviar, weighing

from 100 to 150 pounds each, in a single season. As fishing pressure increased, catches of Polyodon declined. In some areas, paddlefish completely disappeared from waters they had previously inhabited in great abundance. Much of the blame for their decline at that time was laid to the construction of navigation dams since it was felt that they presented an unsurmountable barrier to the migrating fish (Stockard, 1907). Paddlefish populations continued at a low level until the mid 1940's when they began to increase (Carlander, H. B., 1954). Since 1950, the paddlefish have increased until they are common in most of those areas of the Mississippi and Missouri Rivers adjacent to Iowa. The very large fish which were so prevalent during the early fishery make up a very small part of the commercial catch at the present time. Of the commercial take sampled in 1958, the majority of fish ranged between six and ten pounds. Fish in excess of 20 pounds are uncommon today and gravid females are scarce. Nevertheless, during the period from 1947 through 1950, a yield from the Upper Mississippi River of 26,000 to 46,000 pounds was maintained with little evidence of decline (Carlander, H. B., 1954). During 1957, 191,789 pounds were taken from the Mississippi River above Keokuk, Iowa (Proc. Upper Miss. Conserv. Comm., 1958). In the Missouri River adjacent to and above Iowa, commercial fishing pressure has been less intense. In the tailwaters below Fort Randall Dam, Pickstown, South Dakota, paddlefish abound in such numbers that an extensive sport fishery has developed. The catch by anglers using snagging gear at the Fort Randall Dam approached 55,000 pounds during the 1957-58 season (Shields, 1958). Such yields negate the assumption that dams were

responsible for the decline in the early fishery.

Since the present study would be considerably enhanced if it were possible to obtain some young, parasite-free Polyodon, a detailed study was undertaken on the growth, maturation, and reproduction of all fish collected.

MATERIALS AND METHODS

Paddlefish examined in this study were taken by commercial fishermen on the Mississippi River near Burlington, Iowa, or were collected with the aid of survey crews of the South Dakota Department of Fish and Game. Two types of gear were utilized, namely, large mesh gill nets and drag seines. All collections during the months of December through March were made using four-inch bar mesh gill nets set beneath the ice in sloughs and backwater areas of the Mississippi River in Pool 19 near Burlington, Iowa. Collections from the Mississippi River at other times of the year were made using a 1000 foot drag seine having a depth of 15 feet and a mesh size of two inches, bar measure. Collections from the Missouri River were made using large mesh gill nets set in the tailwater areas of Fort Randall Dam near Pickstown, South Dakota only during the months of June, July, and August.

All fish were weighed, measured, and sexed. Weights were recorded to the nearest half-pound, measurements were taken of the total length, the fork length, and the length from the tip of the paddle to the leading edge of the upper jaw. All specimens were sexed and any indication of sexual development was noted. From each fish, a section of the dentary bone was removed from the antero-lateral area of the lower jaw near the symphysis with the aid of a set of bone cutters. The flesh was then stripped from the pieces of bone which were then allowed to dry. Techniques of preparing these bones for study will be discussed in the following section on age and growth.

Several attempts were made to transport live Polyodon to the laboratory where they might be kept in live tanks to serve as a more convenient supply of cestodes. Since attempts to transport the fish in large tubs filled with ice and water were unsuccessful, anesthetics were considered. Sodium amytal has been used successfully in transporting fish to the Salton Sea in California (Reece, 1953; MacFarland, 1954) and was utilized in the next attempt to maintain paddlefish in a living condition. At a concentration of one half grain per gallon of water, individual fish showed great differences in tolerance and it was impossible to develop a suitable technique which was practical for use in the field. Schultz (1956) found that urethane (ethyl carbamate) produced excellent results when used on northern pike and walleyes. He found that anesthetized fish could be packed in ice for from one to five hours with excellent recovery. This compound proved to be unsatisfactory in some of my preliminary experiments and its use was discontinued when it was reported to be carcinogenic. Quinaldine (2-methylquinoline) has also been used as an anesthetic (Muench, 1958). This compound is not readily soluble in water and must be used with acetone to overcome this difficulty. Usually, acetone is added to make an aqueous solution of 1:10,000. Quinaldine is then added to make a treating solution of 5 to 12 p.p.m. This concentration will anesthetize large paddlefish within ten minutes at 75°F. Recovery may take from five to 30 minutes. By packing anesthetized fish in ice, several paddlefish were successfully transported to the Iowa Lakeside Laboratory from the Missouri River, a distance of 204 miles. One fish lived for ten hours after revival from

the Quinaldine treatment, another lived for 20 hours, and a third for 28 hours. Examinations of the dead fish showed multiple hemorrhages in the vicinity of net wounds or showed injuries which might have resulted from handling. It appears that Quinaldine has definite possibilities for further use in investigations of this nature if it becomes possible to secure fish by less rigorous methods.

FOOD HABITS

The peculiar structure of the head of Polyodon spathula has led to much speculation concerning the feeding habits of this species. The paddlefish possesses an enormous mouth, a long, broad spathulate snout and abundant gill rakers (Figs. 30 and 31). Fishermen who are unacquainted with microscopic forms of life have often mistaken partially digested plankton for mud and claim that the paddle is used for digging in the mud to stir up food organisms. Stockard (1907) reported that fishermen in bayous of the lower Mississippi River felt that paddlefish were responsible for large holes that occurred in the bottom of drained lakes which had formerly been heavily populated with paddlefish. Many workers, including Forbes (1878), Jordan and Evermann (1896), Imms (1904), and Alexander (1914) subscribed to this idea.

Many factors can be cited which cast doubt on the above assumption. Numerous food studies over the past 50 years have failed to find mud in the stomachs of any paddlefish examined. Forbes (1888a, 1888b) found many insects, insect larvae, and zooplankters, but no mud. Forbes and Richardson (1908) could find no trace of mud in the stomachs of fish they examined. Eddy and Simer (1929) reported that, except for detritus, stomachs of paddlefish examined in their studies contained only plankton and insect larvae. Stockard (1907) felt that the paddle might be used to stir up soft mud to disturb small organisms which could then be ingested as food. He felt, however, that any mud entering the mouth would pass through the gill rakers and hence, would not be swallowed.

In this way, he explained the abundance of microcrustacea in the stomachs of fish he examined. My studies on the Mississippi and Missouri Rivers show that fish in the two areas have markedly different food habits. See Tables 3 and 4.

Mayfly naiads (Hexagenia and Pentagenia sp.) make up the major bulk of the diet of Polyodon taken from the study area on the Mississippi River. Microcrustaceans are numerous but they make up only a small percentage of the total food volume. In the Missouri River, analyses of stomach contents indicate that paddlefish in that area feed almost entirely upon plankton. In one instance, it was observed that dragonfly naiads were eaten as food. No trace of mud, however, was found in the stomachs of fish from either river.

If the paddle were actually employed in digging so as to stir up food organisms, one would expect it to be scarred and scratched. This is not the case. Furthermore, paddlefish seem to be highly sensitive to blows, pressure, or excessive contact on the paddle. Fish encircled by a seine often give up their efforts to escape after striking the net and float on their backs. Seldom do they back away from the net and continue to resist. It is very unlikely, therefore, that the fish use this structure in such vigorous activity as would be required to agitate the mud to a depth which would disturb the mayfly naiads.

Likewise, if the paddle were essential in securing food, a fish lacking such a structure would be expected to be in poor condition. Fish lacking the snout are common in my collections. Polyodon which have had the paddle removed by trauma, primarily as a result of having been struck

Table 3. Comparison of food items found in the stomachs of paddlefish taken from the Mississippi and Missouri Rivers, 1958-1959

		Adult insects	Immature insects[a]	Cladocera	Copepods	Phyto-plankton[b]	Other
Mississippi River	% by Volume	Trace	95%	1%	4%	Trace	Trace
Mississippi River	% by Number	Trace	60%	10%	30%	Trace	Trace
Missouri River	% by Volume	---	Trace	15%	75%	10%	Trace
Missouri River	% by Number	---	Trace	15%	75%	10%	Trace

[a]Mostly mayfly naiads

[b]Almost entirely Asterionella sp.

Table 4. Tabulation of specific food items based on the frequency of their occurrence in the stomachs of paddlefish taken from the Missouri and Mississippi Rivers, 1958-1959

Organism	Mississippi River	Missouri River
Insects		
Mayfly naiads	A[a]	O[b]
Dragonfly naiads	R[c]	R
Adult insects	R	O
Zooplankton		
Daphnia	C[d]	A
Bosmina	C	A
Leptodora	R	R
Diaptomus	C	A
Cyclops	A	A
Miscellaneous animals		
Hydrachnidae	R	O
Fish	R	O
Plants		
Melosira	R-C	R
Asterionella	O	C
Other diatoms	R	R
Filamentous algae	R	R
Rooted aquatics	O	O
Detritus	R-C	R

[a] A - abundant

[b] O - absent

[c] R - rare

[d] C - common

by the propellers of outboard motors, do not appear to be in poorer condition than those possessing the complete structure. The wounds heal completely and the fish show no adverse after-effects.

A more plausible suggestion for the use of the paddle is that suggested by Nachtrieb (1910), who studied the primitive pores of the paddlefish. He found them to be most abundantly distributed on the head and paddle with many of them on the operculum and others along the lateral line. Herrick (1922) and Norris (1923) felt that the paddle merely provided additional surface for the distribution of these sensory organs, helping the fish to detect the presence of food organisms. This might also explain the peculiar lateral movements of the head made by fish as they swim along. My observations, and those of Kofoid (1900), on feeding paddlefish indicate that, in nature, the fish swim along with their mouths wide open in areas of plankton concentrations and continually move their paddles from side to side as they swim. Kofoid (1900) and Weed (1925) reported that captive fish exhibit the same behavior patterns when fed finely chopped meats. When not feeding, the fish make the lateral movements less frequently and swim with the mouth closed.

Anatomically, Polyodon spathula is best adapted to a mode of feeding involving non-resistant types of food organisms. Its jaws are weak and entirely unadapted for grasping prey. Its gill rakers are long and modifed to form an efficient screening device for the removal of small organisms from the water. Imms (1904) described the gills of Polyodon as "... a straining mechanism which effectually bars the entry ... of microscopical organisms into the gill cavities." Psephurus gladius,

the only other member of the Polyodontidae, he noted, has comparatively short gill rakers which are far less numerous.

Ralph Smith (1958) published the following statement on paddlefish in a popular magazine:

> ... As a practical thing, they cannot be taken on a baited hook. They feed on plankton and other tiny organisms. The fish's coal-scuttle mouth is equipped with a series of modified gill rakers which strain out microscopic bits of food, as jaws agape, the fish moves through the water. For a paddlefish to swallow even a small minnow, compared to its usual fare, would be approximately the equivalent to a human being swallowing a whole hog in one gulp! ... [Underscoring mine.]

Evidence is available, however, that paddlefish not only are able to, but actually do swallow larger organisms. Paddlefish in the Mississippi River commonly feed on large mayfly naiads which are definitely not microscopic. In addition, one two and a half inch fish, probably a river darter, Percina shumardi (Girard), was found in the stomach of a paddlefish taken in 1958. Forbes (1888) also found that Polyodon occasionally take fish. Biologists of the Iowa Conservation Commission once placed a number of large paddlefish into a rearing pond stocked with several hundred fingerling trout. The following morning, few fingerlings remained and all paddlefish were gorged with the small trout. Not only were the paddlefish capable of swallowing the trout, but they were also very efficient in capturing them (E. B. Speaker, personal communication, 1958). Such a graphic example suggests that Polyodon might be a capable predator under natural conditions. Even though paddlefish are common in the tailwaters of large dams where huge schools of minnows congregate, food studies indicate that they normally do not feed on fish.

Beach (1902) reported that, in feeding, Polyodon spathula elevated the paddle above the water and used it to force aquatic plants into its mouth. Any organisms jarred from the plants would then float into the posterior branchial region and be swallowed. Norris (1923) included a similar hypothesis and added that the mode of swimming of Polyodon would aid in dislodging such food organisms. Forbes (1888) believed that since the stomachs of paddlefish contain many microcrustaceans but no mud, the fish must be able to separate zooplankton from the mud or algae or must drive the microcrustaceans out of the vegetation where it can be caught. Such phenomena seem highly unlikely for two reasons. First, I have neither observed nor collected paddlefish from areas of dense vegetation. Secondly, such activity would surely cause some plant material to be swallowed accidentally. This has never been observed in any of the stomachs I have examined. Furthermore, the lateral movements of the paddle, accompanied by rhythmic movements of the body often occur during swimming, regardless of the presence of vegetation (Eddy and Simer, 1929). It would seem, therefore, that these actions represent a normal behavior pattern for the fish.

In areas where paddlefish are abundant, the fish frequently are observed to leap completely out of the water. Local fishermen claim that this is an action taken by the fish to rid themselves of lampreys which are parasitizing them. In my studies, this behavior was observed many times but not a single lamprey wound was found on any of the fish examined in the past three years. Fish have been observed swimming just

beneath the surface on such occasions and it seems that they leap for sport rather than for any other reason.

SPAWNING ACTIVITY

No authenticated observations of the spawning behavior of Polyodon spathula are reported in the literature. C. R. Stockard (1907) spent extended periods in 1904 and 1905 searching for the spawning areas of this fish. At that time, populations of paddlefish were high and gravid fish made up a considerable portion of the commercial catch. Even though he consistently was able to take ripe fish, Stockard never succeeded in observing them spawn. At the end of his unsuccessful search, it was his belief that paddlefish spawned at the mouths of small bayous which were filled with running water. He believed that fish migrated out of the quiet waters of lakes to spawn. Such migrations then, he proposed, were the basis for the "spring runs" and also explained why Polyodon catches declined in lakes which had been cut off from their original supply of flowing water.

D. H. Thompson (1933) reported the observations of a commercial fisherman who felt that he had seen the spawning activity of paddlefish but details are lacking. James E. Kurrle, Jr. (personal communication, 1958), tells of taking a very large gravid female in a wing net set on a sand bar in April, 1948. The net was filled with many other smaller fish, all of which were males. Apparently, other males had frantically attempted to reach the female and many of them had gilled themselves in the netting leading to the purse. Mr. Kurrle indicates that all fish involved were sexually mature.

Today, gravid females are uncommon, even among large fish, taken

in the Mississippi River. During the development of the paddlefish fishery, however, an extensive market developed for the roe of this species to help meet the demand for sturgeon caviar. Fishermen were reportedly able to ship as many as 11,250 pounds of caviar per fisherman in an average season during the early 1900's (Stockard, 1907).

The scarcity of very young paddlefish and the occurrence of gravid females led to attempts to hatch the eggs of Polyodon artificially. Adults collected by L. H. Bennett (personal communication, 1958) from the Mississippi River at Fairport, Iowa were maintained in large hatchery ponds in the hope that they would mature. After waiting several years without success, the fish were released. At the time of release (June), one female was found to be gravid and discharged eggs from the vent. Attempts to locate a mature male failed and the female was liberated. C. A. Purkett (personal communication, 1958) took ripe fish from the Osage River in Missouri in early April, 1958. He succeeded in collecting fertile eggs but was unable to keep the embryos alive due to a lack of proper facilities and equipment.

My collections included gravid fish taken during the months of January, February, April, June, and September. In these specimens, all of the ovaries contained dark black eggs which appeared normal and nearly mature (Fig. 35). W. F. Allen (1911) collected gravid fish in March and early April but found that only large fish weighing over 15 pounds attained sexual maturity. He collected small paddlefish during July, August, and September but was unable to find any concrete evidence of spawning activity even though he spent the entire summer searching for

naturally-spawned eggs or newly-hatched Polyodon. Alexander (1914) was able to take mature fish in February, March, and early April. He reported that gravid females were scarce in his catches and, when present, weighed only eight to ten pounds. J. T. Shields (personal communication, 1958) collected sexually mature fish which were even smaller. He found that males as small as five pounds were ripe and that females as small as six and one half pounds were gravid.

In this study, histological preparations of gonads from both sexes of paddlefish, taken at various seasons of the year, were prepared. In seven females, ranging in size from 5.5 to 20.0 pounds, no differences in the development of the eggs could be detected, even though several of the specimens were collected in late April when it is believed that the species normally spawns. (See Figs. 36-39). Studies on the testes indicate that male Polyodon show no sexual activity before they are seven years old. At any season thereafter, it is possible to find mature spermatozoa within the tubules but none of the male fish examined in this study exhibited a high level of sexual activity. (See Figs. 40-44). It seems likely, therefore, that individual paddlefish do not spawn annually. Instead, they appear to spawn at irregular intervals of from four to seven years, as suggested by the bands of crowded annuli observed in sections of the dentary bone. Such bands are discussed in a later section of this paper.

At infrequent intervals, the pronounced migrations of paddlefish reported by Stockard (1907) still occur. Such a migration occurred in the spring of 1959 in Pool 19 of the Mississippi River near Burlington,

Iowa. Fishermen of the area reported that this was the first such "run" in the last decade although older fishermen remember such phenomena at infrequent intervals in the past. In April, 1959, commercial fishermen in Pool 19 took thousands of pounds of paddlefish in less than ten days. Catches were so large that the supply exceeded the market demand and many fishermen attempted to maintain the fish in large holding tanks. This provided an excellent opportunity to study the composition of the run. All ages and sizes of fish were represented with nearly equal numbers of males and females. Workers at the market report that none of the thousands of Polyodon taken at that time was found to be mature when dressed. All of them, however, were gorged with mayfly naiads. A check on river conditions at the time indicates that the area in which the fish had congregated had become cleared of ice approximately 24 hours before the "run" began. The change in water temperature, coupled with the removal of the ice may have been responsible for the migration, but this has not been substantiated. The absence of sexually mature fish in the "run" suggests that some factor other that spawning initiated the behavior.

FECUNDITY

In two instances, it was possible to study the ovaries of gravid female Polyodon. Commercial fishermen collected two large females and preserved the ovaries for study. Vital statistics on these fish are lacking other than the fact that both fish were approximately 54 inches in length and weighed over 25 pounds. One fish was taken in January, the other in February, 1958. In general, the left ovary of Polyodon, is larger than the right. Each ovary was, therefore, examined separately.

Following their removal from the fish, the ovaries were placed into large jars and preserved in ten per cent formalin. After allowing the eggs to harden for ten days, the ovaries were removed from the jars, washed in tap water, and allowed to drain. The volume of each ovary was then determined as accurately as possible.

To compute the volume, each ovary was immersed in a known quantity of water contained in a 1000 cc. cylinder, graduated at ten cc. intervals. Whenever the volume did not fall upon a marked level, additional water was added from a ten cc. burette to bring the total volume up to such a point. By subtracting the total amount of water from the final reading, it was possible to obtain a sufficiently accurate value for the volume of an ovary. Three separate volumetric determinations were made on each ovary and the average of these was used in further computations. A procedure similar to that described above, but on a smaller scale, was applied to samples from each ovary. The number of eggs in

these samples was counted and converted into number of eggs per cc. Portions from all areas of the ovary were included in each sample to avoid any bias should the size of eggs vary within the ovary. Determinations were made on three such samples and the average was used to extrapolate. The total number of eggs in a particular ovary was determined as the product of the volume and the number of eggs per cc. Following such a determination, the eggs in one ovary were counted individually as a check on the technique. Such a check indicated that the error due to technique was less than three per cent. The actual number of eggs in the ovary subjected to this examination was 66,107. The number obtained using the volumetric determination was 67,826. By applying the technique to the remaining ovaries, these results were obtained:

Fish No.	Right Ovary	Left Ovary	Total Eggs
1	67,676	74,855	141,531
2	66,107	71,140	137,247

The ovaries included in these determinations contained large, heavily pigmented eggs, similar in appearance to those described by Roussow (1957) for Acipenser fulvescens. The size of eggs in the ovaries examined was essentially uniform. The ovary taken from Fish No. 1 contained 88.4 eggs per cc. whereas that from Fish No. 2, taken one month later contained 85.3 eggs per cc.

MORPHOMETRY

Paddle-length to Total-length Relationship

During the course of this study, the relationship of paddle-length to total body length was investigated. Data from my field observations were supplemented with data from the literature when the necessary statistics were provided. The works of Thompson (1934) and of Stockard (1907) supplied information on very small and very large Polyodon, respectively.

Data from 240 Polyodon, ranging in size from 0.67 inches (17 mm.) to 85 inches, are included. Although certain sizes appear most frequently in commercial catches, the fish included in this analysis are well distributed over the size range. Thompson (1934), in his study on the relative growth of Polyodon, included measurements from many fish and computed the relationship of the paddle-length to the length of the remainder of the body. Using a logarithmic scale, he found that the distribution of such values suggests a curvilinear relationship. As reference points, Thompson measured the snout as the distance from the tip of the paddle to the anterior edge of the eye. In my studies, I measured the distance from the tip of the snout to the medial edge of the upper jaw. An examination of various sizes of fish indicates that these reference points do not differ and the data were therefore combined.

A straight-line regression of paddle-length on total length derived from the study of the 240 specimens is expressed by the formula:

$Y = 0.2366\ X$ plus 1.48 inches

where X equals the total length in inches and Y equals the paddle length in inches. This relationship immediately indicates the absurdity of a fish of zero inches in length having a paddle measuring 1.48 inches. Nevertheless, when the data are plotted on a graph and the regression line is fitted, the agreement between the two is generally good (See Graph 1). An r value of 0.988 emphasizes the close relationship between the data. The points representing very small fish (i.e., those less than ten inches in length) or very large fish (those over 72 inches) suggest that a curvilinear relationship would provide a better description. The regression for those fish measuring less than ten inches in total length follows the formula:

$Y = 0.3650\ X - 0.18$ inches $\quad r = 0.986$

Sufficient specimens are not available for any investigation of the relationship between the length of the paddle and the total length of fish over 72 inches.

Length-weight Relationship

It has been shown that the length-weight relationship of fish is curvilinear and is best expressed in logarithmic terms (Hile, 1936; LeCren, 1951) as $\log W = n \log L - \log a$ where W equals the weight in pounds, L equals the length in inches, and a and n are constants. Fish were grouped in intervals of two inches and the mean weight for each group was determined. Using the midpoints of the intervals and the mean weights, the length-weight relationship was computed. The formula

fitting the data from the Mississippi River is expressed as log W = 2.84250 log L - 3.63867. The relationship for the Missouri River follows the formula log W = 3.46452 log L - 4.60497. These lines are fitted to their respective data in Graphs 2 and 3.

Condition Factors

Using the formula $W = CL^3$, condition factors ("C" values) were computed for all fish. No seasonal difference is evident in the condition factors (Table 5). Condition factors for paddlefish from the Missouri River increase with increases in length, indicating that longer fish are heavier for their length than are short fish (Table 6). Such a trend is not shown by paddlefish from the Mississippi River. When large fish of equal sizes from the two rivers are compared, it is noted that fish from the Missouri River are proportionately heavier than those from the Mississippi River.

Possible explanations for this difference between the two rivers might be found in the food habits of fish in the respective areas. In the Mississippi River, mayfly naiads make up the bulk of the diet, whereas in the Missouri River, zooplankters are the major food item. It would seem, therefore, that either the fish are more capable of utilizing the planktonic forms or that food is more available in the Missouri River.

Table 5. Comparison of coefficients of condition for paddlefish taken from the Mississippi River at different seasons of the year (winter and spring, upper line; summer and fall, lower line)

Length in inches	Number of fish	Mean "C" value	Range
21-25	2	13.3	13.3
	4	13.3	10-15.0
26-30	4	14.8	12.0-17.0
	8	15.5	12.0-22.0
31-35	10	12.2	9.0-18.0
	10	12.5	9.0-16.0
36-40	136	11.5	9.0-17.0
	12	11.8	9.0-23.0
41-45	42	13.3	10.0-20.0
	2	12.0	11.0-13.0
46-50	11	13.0	11.0-15.0
	4	12.8	12.0-16.0

Table 6. Comparison of coefficients of condition for paddlefish taken from the Mississippi (upper line) and Missouri (lower line) Rivers

Length in inches	Number of fish	Mean "C" value	Range
16-20	1	17.0	17.0
	2	7.5	7.0-8.0
21-25	6	13.3	10.0-14.0
	8	10.4	8.0-14.0
26-30	12	14.9	12.0-22.0
	24	12.0	9.0-25.0
31-35	20	12.3	9.0-18.0
	56	12.4	9.0-29.0
36-40	143	11.5	9.0-23.0
	54	12.8	9.0-22.0
41-45	44	13.3	10.0-20.0
	27	14.9	9.0-21.0
46-50	15	12.9	11.0-15.0
	17	17.0	14.0-23.0
51-55	4	17.8	15.0-26.0
	12	16.7	13.0-24.0
56-60	0	----	----
	4	21.3	16.0-23.0

AGE AND GROWTH

The use of calcified structures such as bones, scales, and otoliths as aids in determining the age of fish is a common procedure in fishery research. Numerous studies have demonstrated the validity of this technique and its application has been widespread. Excellent reviews concerning the aging of fish may be found in the works of Heincke (1904), Mohr (1927), and Graham (1929). In addition to the above mentioned structures, the centra of vertebrae, the opercle, subopercle, coracoid, scapula, urostyle, epural, hypural, and hyomandibular bones have been utilized. Techniques for the preparation and analysis of these structures are provided by Holzmayer (1924), Graham (1929), Adams (1931), LeCren (1947), and Menon (1950).

That sturgeon may be aged with a high degree of accuracy from cross-sections of the pectoral fin rays has been shown by many workers (Chugunov, 1925). Using fish of known age, Holzmayer (1924) was able to verify the results he obtained from studying the annuli on sections of the pectoral fin rays. Chugunov (1925) refined this technique and recommended that sections of 0.5 mm. in thickness be cleared and mounted in balsam. Probst and Cooper (1954) found that cross-sections of fin rays provided indices to the age of lake sturgeon (Acipenser fulvescens) as old as 82 years.

Since the use of soft fin rays had been shown to be valid for aging fresh-water fishes (Boyko, 1946) and had been applied with considerable success to sturgeon by Guerrier and Roussow (1951) and Roussow (1955a,

1955b, 1957), it was thought that, in the present study, the use of these structures would provide an index to the age of paddlefish. Pectoral fin rays were removed from all Polyodon collected on the first two trips to the Mississippi River in 1958. Adjacent fin rays did not exhibit the same number of annuli. Furthermore, on many fin rays no annuli could be observed, suggesting that these rays might have been regenerated. This seemed unlikely, however, due to the frequency of such rays, particularly since all of them would have been regenerated within the past year. Of the six to eight rays forming the leading edge of the pectoral fin, it was not unusual to record a different number of annuli on each ray. This condition removed all confidence in the method and another means of aging paddlefish was sought.

Adams (1931, 1942) attempted to use otoliths for aging Polyodon. These structures, he found, were satisfactory only for aging young fish, since sections of otoliths from old fish presented such a blurred picture that it was impossible to separate the annuli. During the present study, otoliths were removed from a variety of sizes of paddlefish taken from the Mississippi River. These otoliths were sectioned at approximately one half millimeter thickness and cleared in xylol. For fish less than five years in age, this structure provided reliable results. Fish older than five years, however, presented a blurred picture similar to that reported by Adams (1942).

Lagler (1956) reports that Polyodon carry minute scales on the caudal peduncle near the base of the tail. Although many specimens were examined in this study, no scales were ever found. It is entirely pos-

sible, however, that they might have been lost in handling the fish prior to examination.

After finding that otoliths were not reliable for aging paddlefish, Adams (1942) turned to the only other calcified structure in the body of the paddlefish, namely the dentary bone. Using sections of this structure he thought he was able to identify the annuli with accuracy and presented an interpretation of the age and growth of Polyodon. Dentary bones were also collected from paddlefish in the present study. One disadvantage of this technique is that it necessarily involves killing the fish.

In determining the most suitable area on the mandible for studying annuli, a complete dentary bone was removed from a 41.5 pound female measuring 54.5 inches in total length. Sections for comparison were taken at one inch intervals along the entire length of the bone (Fig. 34). It was found that the area best suited for study is in the zone of greatest curvature. The postero-lateral portions of the dentary bone are incompletely ossified and the zone in the vicinity of the symphysis is distorted due to the presence of many blood vessels. The contours of the bone change considerably from the anterior to the posterior regions as may be seen in Fig. 34. Much variation in the size and shape of the dentary bone is evident between individual fish. This is due to differences in the number of blood vessels in the central area and in the degree of ossification. These latter factors make it impossible to compute or derive a precise back-calculation of lengths at preceding annuli.

Examination of the dentary bones from various small-sized paddle-

fish, ranging between four and 15 inches, indicates that the dentary bone appears as a simple band of dermal bone along the anterior margin of the lower jaw. This thin band of bone may be removed only with difficulty. At its dorsal edge appears the original Meckel's cartilage containing numerous blood vessels and forming an approximate 60°angle with the slender strip of bone. Meckel's cartilage rapidly becomes overlaid with dermal bone and the shape of the definitive dentary bone is thus established. Both Meckel's cartilage and its associated bony structures are visible in good preparations of the dentary bone from fish of any size. (See Fig. 32). At the posterior ends of the jawbone it is possible to find areas where the fusion is incomplete and separate bones may be visible in these areas. Designation of the first annulus is difficult. In this study, it is defined as the first layer of bone which completely surrounds both Meckel's cartilage and its associated strip of dermal bone. See Fig. 32. The lack of adequate data from small-sized fish makes it impossible to completely verify the mode of dentary bone formation suggested above.

To prepare a dentary bone for study, cross-sections were cut using a Dremel Moto-tool equipped with dental saws. While any section through which light may be transmitted can be aged, thicknesses exceeding one half millimeter are not satisfactory. In such sections, definition of the various annuli is poor and the differentiation between closely crowded annuli may be impossible. Optimal conditions for reading the annual rings are presented in sections approximately three eighths millimeter in thickness. Sections whose cut surfaces are not parallel

present no problems in aging unless the angle is extreme. Sections cut at oblique angles to the axis of the dentary bone do not interfere with readings, but such sections make accurate back-calculations impossible.

Various clearing media were employed. For old fish whose bones are heavily calcified, xylol transmits light well and allows good differentiation of the annuli. In young fish, however, this fluid may clear the bones excessively, making it impossible to read the annuli. For such specimens, the use of glycerine is recommended.

Various types of lighting will produce good results. Transmitted light from an arc lamp equipped with a blue filter is preferred although sections may be aged equally well with reflected light. If sufficiently thin sections can be prepared and mounted in balsam on a microscope slide, the use of a microbeam projector is helpful. Such sections, however, are difficult to cut and mounts of this type require so much time that the use of the microbeam projector is impractical.

Annuli appear on sections of the dentary bone as alternating bands of light and dark areas. The wide, light-colored bands are interpreted as having been formed during the rapid summer growth, whereas the narrow dark bands represent the slower winter growth. The age of a fish may thus be determined by counting either the number of dark bands or the number of complete light bands. Determination of the first annulus was described in the preceding discussion on the formation of the dentary bone.

Biologists from several states have been studying the age and growth of Polyodon in recent years. On February 3 and 4, 1960, workers from

Iowa, Missouri, and South Dakota met in Ames, Iowa to compare techniques for reading dentary bones and to discuss results. Participating were C. A. Purkett (Missouri), James Sprague (South Dakota), Fred Meyer and Dr. Kenneth Carlander (Iowa). Readings by the various workers were in excellent agreement. Interpretations of age usually differed by one or two years, rarely three or more, on fish whose ages ranged as high as 25 years. In studying dentary bones from fish of a wide range of ages, it became apparent that in fish older than ten years, the innermost annuli often become vague and indistinct. As the age of the fish increases, more and more annuli become incorporated into this central area and careful examinations are required to distinguish them. At times, curious "halo-like" markings occur outside certain annuli. Such marks are not considered to be true annuli unless they can be followed extensively in lateral directions. No explanations of their occurrence can be offered at this time.

Lengths of paddlefish at various ages as determined from annuli on the dentary bones are presented in Table 7.

Evidence of accuracy of estimating the age of fish younger than five years was shown by close agreement between readings from otoliths and from dentary bones. As stated previously, it was impossible to utilize the otolith for aging fish older than five years.

Additional support for the estimated ages was provided when the sizes of fish at each annulus were compared with length-frequency tables. Again, the techniques seem in agreement. In 1957, commercial fishermen in Pool 19 of the Mississippi River reported a large number of small

Table 7. Total lengths in inches of paddlefish from the Mississippi River, 1956-1959, by age groups as determined from dentary bones

Age group	Year collected	Number of fish	Mean length	Length range	Mean weight	Weight range
0	---	---	---	---	---	---
I	1959	1	8.1	8.1	---	---
II	1956	6	21.8	18.2-23.5	1.6	1.0-2.0
	1959	1	18.0	18.0	---	---
III	1956	11	27.9	24.5-31.5	3.3	2.0-5.5
	1958	4	30.0	29.0-31.0	3.0	3.0
IV	1956	2	31.8	30.5-33.0	6.0	6.0
	1958	14	34.5	33.0-35.0	4.5	3.5-6.0
V	1958	25	36.0	34.0-37.0	5.6	4.5-7.0
	1959	1	36.5	36.5	6.5	6.5
VI	1956	1	36.6	36.6	9.5	9.5
	1958	73	38.1	34.0-39.0	6.3	5.0-7.5
VII	1958	20	39.5	38.0-41.0	7.4	6.0-8.5
	1959	4	39.9	39.0-41.0	7.3	6.5-9.0
VIII	1958	17	40.4	39.0-42.0	7.9	7.0-9.0
	1959	2	39.8	39.5-40.0	10.3	9.5-11.0
IX	1958	12	42.0	40.0-44.0	9.1	8.0-10.5
X	1958	6	42.9	41.0-44.0	12.3	9.0-14.0
	1959	3	42.5	42.5	12.8	11.0-13.5
XI	1956	1	43.5	43.5	9.5	9.5
	1958	9	43.6	40.0-45.0	11.7	10.0-14.0
XII	1958	9	45.2	44.0-47.0	11.9	11.0-13.0
XIII	1958	6	46.3	45.0-47.0	12.3	11.5-13.0
XIV	1958	3	47.3	46.0-48.0	13.5	13.0-14.0
	1959	2	46.8	46.5-47.0	18.0	18.0

Table 7 (Continued)

Age group	Year collected	Number of fish	Mean length	Length range	Mean weight	Weight range
XV	1958	5	48.2	45.0-49.5	16.3	16.0-16.5
XVI	1959	1	48.0	48.0	19.5	19.5
XVII	---	---	---	---	---	---
XVIII	---	---	---	---	---	---
XIX	1958	2	51.0	51.0	21.0	19.5-22.0
XX	1958	1	51.0	51.0	19.5	19.5
	1959	1	52.0	52.0	25.0	25.0
XXI	---	---	---	---	---	---
XXII	1958	1	54.5	54.5	25.0	25.0
	1959	1	54.0	54.0	41.0	41.0

Polyodon in their catches. These fish measured approximately 36 inches and weighed approximately 5.5 pounds. Since the minimal legal limit in Iowa is five pounds, this group of fish caused much consternation to the fishermen. In 1958, these fish were still very much in evidence, their size having increased to 38 inches and their weight to about 6.5 pounds. Collections made in 1959 indicate that these fish now measured 39.5 inches and weighed over seven pounds. It is assumed that these fish represent a single year class. This interpretation must be tempered with the knowledge that many paddlefish show peculiar clumpings of annuli on their dentary bones. The first such grouping often occurs around the seventh or eighth annulus, a condition which might account for the massing of fish in the 38 inch group. Since recruitment occurs at the five pound weight level, the large group of fish reported in 1957 may also be of doubtful significance.

L. A. Adams (1942) listed the following estimates of growth based upon cross-sections of the dentary bones of paddlefish taken in his area: (lengths given in inches)

I	7 to 12	VII	39 to 40
II	18 to 27	VIII	not given
III	28 to 32	IX	42
IV	33 to 36	X	42 to 46
V	37	XI	not given
VI	38	XII	47

An attempt was made to back-calculate the sizes of fish at various annuli. The changing configuration of the dentary bone along its length

precludes the determination of a valid body length-dentary bone relationship. The derivation of such a formula would require sections from corresponding areas of the dentary bone of each fish, with each section cut at a right angle to the longitudinal axis of the bone. Although a precise technique of this sort is not feasible at this time, such computations might be valuable in indicating the validity of results obtained by other methods. In Table 8 are some of the values calculated for the sizes of fish at each annulus, assuming a direct proportion relationship between the growth of the bone and the length of the fish.

During the examination of sections of the dentary bones of large Polyodon, all over five years of age, peculiar crowding of annuli was noted. This phenomenon, as previously noted, recurred at intervals of four to seven years and indicated an interruption of the normal pattern of growth (See Fig. 33). In preliminary studies of sections of the dentary bone, no significance was ascribed to such areas which indicate a pronounced retardation of growth. A study by George Roussow (1957) indicated that a similar phenomenon was also evident in sections of the fin rays of lake sturgeon, Acipenser fulvescens Rafinesque, taken in the province of Quebec. In his studies, Roussow showed that such "belts," as he called them, are produced in both sexes. These are particularly noticeable in female fish when yolk materials are added to the ova. At this time, nutrients are utilized primarily for developing the eggs and for body maintenance, rather than for growth. My records of ripe or gravid female paddlefish over the past four years indicate that annual spawning does not occur. In 1958, a few gravid fish were taken at

Table 8. Back-calculated lengths (in inches) at each annulus of five paddlefish from the Mississippi River

Annulus	Fish No. 1	Fish No. 2	Fish No. 3	Fish No. 4	Fish No. 5
1	5.0	4.2	5.2	5.2	6.6
2	13.2	15.7	15.7	13.5	12.2
3	21.0	22.0	21.0	21.6	21.4
4	29.6	26.2	28.5	28.0	26.0
5	34.3	34.5	32.0	33.5	33.2
6	36.0	---	36.0	36.5	37.0
7	38.0	---	---	38.0	39.0
8	38.5	---	---	---	---
9	40.3	---	---	---	---
10	41.6	---	---	---	---
11	43.0	---	---	---	---
12	43.5	---	---	---	---
13	45.0	---	---	---	---
14	47.3	---	---	---	---
15	48.0	---	---	---	---
16	49.0	---	---	---	---
17	49.8	---	---	---	---
18	51.0	---	---	---	---

scattered intervals, including January, February, June, September, and October. In 1959, of the thousands of fish taken from a "run" by commercial fishermen in Pool 19 of the Mississippi River, none contained eggs in any advanced stages of development. For these reasons, it seems likely that the periodic occurrence of crowded annuli in paddlefish is associated with spawning activity.

By plotting the length at each annulus against the age of a fish, a graph similar to that provided by Roussow (1957) results. See Graph 4.

Except for post-larval Polyodon collected only by Thompson (1933) and his associates, fish of known age have not been secured, and estimates of first year growth have ranged from six inches as proposed by my data to 32 inches as reported by Houser and Bross (1959). Because the early stages are so rarely seen, most of the evidence supporting the various estimates is of a circumstantial nature and may be subject to considerable error. While much variation is known to occur between populations, it is difficult to reconcile the differences between my findings and those of Houser and Bross. The records of small sized Polyodon are summarized in Table 9.

When the collection records given above are charted on a date-length relationship, several significant factors become evident. The occurrence (Graph 5) of four to seven inch paddlefish in September as compared to six to 12 inch fish taken in July immediately suggests two different age groups. Sections of the dentary bones removed from the paddlefish in the Iowa State University Fish Collection, as listed in Table 9, indicate that those fish collected in September, 1942 (4.1 to 7.0 inches,

Table 9. Reported collections of small Polyodon

Date	Number of fish	Size	Reference
May, 1932	7	0.7-0.8 inches	Thompson, 1933
May, 1944	?	0.7-0.8	Thompson, personal communication, 1958
? ?	1	1.4	Barbour, 1911
September, 1854	7	1.5-4.2	Barbour, 1911
July, 1936	200	2.5-3.2	Aitken, personal communication, 1958
July, 1910	3	2.9-3.6	Danforth, 1911
July, 1904	25	4.0-6.0	Allen, 1911
September, 1942	4	4.1-7.0	Iowa State University, Fish Collection
? ?	1	5.6	Personal collection, Fred P. Meyer
? ?	1	7.8	Adams, 1942
July, 1959	1	8.1	Iowa State University, Fish Collection
July, 1939	1	8.2	Iowa State University, Fish Collection
July, 1940	5	6.0-12.0	Iowa State University, Fish Collection
Aug. & Sept., 1910	?(many)	6.0-12.0	Danforth, 1911
Feb. & Mar., 1930	?(many)	7.9-12.0	Thompson, 1933

total length) show no annuli, whereas those collected in July, 1939 and 1940, (6.0 to 12.0 inches, total length) show one annulus. The relationship shown in Graph 6 is similar to that of Graph 5 and indicates an increased growth rate during the second year which is not evident in the former.

A single small paddlefish (Fig. 29) was taken in the Mississippi River in July, 1959, on a trot-line baited with Ivory soap and set in the channel of the river. This specimen, measuring 8.1 inches, represents the smallest Polyodon collected in this study. Its dentary bone shows one annulus.

Due to the use of commercial fishing gear for obtaining many of the specimens included in their report, it is very likely than an extreme gear bias exists in the collections of Houser and Bross (1959). During three years of commercial fishing in Pool 19 of the Mississippi River, fishermen took no paddlefish smaller than 17.5 inches in the gear they employed to take this species, even though they took as many as 1500 pounds of Polyodon in a single day. Yet during this time, young or smaller paddlefish must have been present because of continued recruitment throughout and subsequent to that period. Gear normally employed in commercial fishing will not take small paddlefish and lake survey crews seldom take any of this species unless they specifically set out to do so. It is entirely possible, therefore, that the missing year classes in the collections of Houser and Bross taken from Fort Gibson Reservoir, Oklahoma, are merely too small to be taken in the gear presently in use.

HOST-PARASITE RELATIONSHIPS

Since Polyodon spathula attains a large size and considerable weight, few predators are capable of feeding on this species after its first year of life. Dietary preferences of the paddlefish are such that, except on rare occasions, other vertebrates seldom are ingested. Consequently, any intestinal parasite of Polyodon would of necessity be one whose life cycle was direct, or one whose intermediate host would have to be an invertebrate. Only microcrustaceans and immature insects are commonly found in the stomach contents of paddlefish from the Missouri and Mississippi Rivers.

Marsipometra hastata utilizes the copepod, Cyclops bicuspidatus, as an intermediate host in its life cycle. This organism is abundant in areas commonly inhabited by paddlefish and is eaten by them in large numbers. The cestodes release tremendous numbers of eggs in the spring soon after the temperature of the water approaches 62°F. and disappear from the intestine soon afterwards. Hatching of the cestode eggs occurs immediately after they reach the outside of the host body. Correlated with the seasonal release of the tapeworm eggs in early spring is the schooling behavior of Polyodon at this same time. The large concentrations of fish at a time when egg release is at its maximum permits higher concentrations of eggs in a less widely distributed area. This concentration of coracidia raises the number of larvae per unit of water and thus enhances the possibility that they will be encountered and eaten by the copepod host.

Feeding habits of the paddlefish are relatively constant. Even though zooplankters are eaten throughout the year, a paddlefish cannot become parasitized until Marsipometra plerocercoids within the Cyclops have developed to an infective stage. Following this requisite developmental period, paddlefish within a short time may develop infections involving thousands of immature tapeworms. In nature, this period of infection occurs during the latter weeks of August. Additional worms may be acquired throughout the fall. As a consequence, a paddlefish harbors many worms of approximately the same stage of development as well of lesser numbers of varying sizes.

Differences in food habits apparently affect the size of the parasite burden carried, even though fish from either river are heavily parasitized and infections may involve several thousands of worms. Individual specimens of Polyodon collected in the Mississippi River consistently harbor several hundred to a thousand fewer tapeworms than do those from the Missouri River. This is probably related to the fact that only approximately five per cent of the volume of the stomach contents of paddlefish from the Mississippi River consists of zooplankters. The remaining 95 per cent of the volume is made up of mayfly naiads. Conversely, at the Missouri River, immature insects are uncommon in the stomach contents of paddlefish. Such differences may well explain the variation in the levels of infection.

SUMMARY AND CONCLUSIONS

1. Various stages in the life history of Marsipometra hastata (Linton, 1898) Cooper, 1917, a pseudophyllidean cestode found in the paddlefish, Polyodon spathula (Walbaum, 1792), have been reared in the laboratory.

2. During the months of April and May, tapeworms in the intestine of the paddlefish mature rapidly and release large numbers of eggs which are expelled with the feces.

3. Hatching requires the stimulus of contact with fresh water and is retarded by low temperatures. At levels below 61°F., hatching is greatly reduced.

4. The coracidia closely resemble those of other pseudophyllidean tapeworms. Their activity and life span are directly affected by water temperatures. At temperatures below 55°F., little or no activity can be observed, although the larvae may be maintained under these conditions for prolonged periods of time.

5. The copepod, Cyclops bicuspidatus, serves as an intermediate host for Marsipometra hastata. Evidence is provided which suggests that additional hosts are not required.

6. Coracidia are ingested during normal feeding activities of Cyclops and onchospheres appear in the haemocoel within eight hours after

their ingestion. The embryonic hooks are lost during this interval.

7. Early development beyond the onchosphere stage is rapid. Several hours after reaching the haemocoel, the larvae change from a spherical shape to a berry-like mass of cells. By the end of four days they have doubled in size and begin to elongate.

8. A normal procercoid stage is not formed. None of the larvae observed developed a cercomer.

9. Two weeks post-ingestion, the larvae are elongate and sausage-shaped. Subsequent development involves an increase in size with little change in shape.

10. After developing in the copepod for 55 days, larvae show concentrations of nuclei at one end which might suggest the beginning of a rudimentary scolex.

11. Further experimental studies on the life history could not be carried on because of the unavailability of parasite-free Polyodon. In nature, infective plerocercoids develop by mid-August and large numbers of juvenile worms appear in the intestine of the paddlefish at that time. The smallest cestodes recovered from naturally-infected fish are only slightly larger than those developed in laboratory-reared copepods.

12. A study of the morphology of the three previously described species of Marsipometra was undertaken. Of these, M. parva is accepted as

a valid and separate species. A careful comparison of type specimens of M. hastata and M. confusa with material collected in this study indicates many similarities between the two. Evidence is provided to suggest the feasibility of reducing M. confusa to synonymy with M. hastata.

13. A complete study of the food habits of paddlefish, as shown by stomach contents, was conducted on fish collected from the Missouri and Mississippi Rivers. In the former, zooplankters form the bulk of the diet. In the latter river, mayfly naiads are the major food item.

14. Attempts to study the spawning behavior of Polyodon were unsuccessful. Evidence based upon histological studies, growth studies, and field observations suggests that individual paddlefish do not spawn annually, but appear to do so at irregular intervals varying from four to seven years.

15. In gravid female paddlefish, the left ovary is larger than the right. A 25 pound female will produce approximately 140,000 eggs.

16. The relationship of paddle-length to total-length follows the formula: Y = 1.48 inches plus 0.23660 X.

17. Old fish in the Missouri River are heavier than fish of similar size from the Mississippi River. The length-weight relationship is expressed by the logarithmic formula:

$\log W = 2.84250 \log L - 3.63867$ for the Mississippi River, and

$\log W = 3.46452 \log L - 4.60497$ for the Missouri River.

18. A comparison of condition factors between the two rivers shows that old paddlefish in the Missouri River are proportionately heavier than young fish in that area. This is not evident in the Mississippi River. No seasonal trend in condition factors was noted.

19. Various techniques for aging paddlefish discussed and compared. The use of pectoral fin rays is considered unreliable for determining age. Cross-sections of the dentary bone provide the most reliable information.

20. The structure of the dentary bone is discussed and a method for its formation from Meckel's cartilage and dermal bone is suggested.

21. Annuli in the dentary bone of paddlefish are defined as distinct continuous layers of calcified bone beyond the initial layer encompassing the first strip of dermal bone and Meckel's cartilage.

22. It has been impossible to obtain fish of known age. However, various techniques, including length-frequency tables, dominant year classes, sectioned dentary bones and back-calculations are employed to support the interpretations of age ascribed to individual paddlefish.

LITERATURE CITED

Adams, L. A.
1931. Determination of age in fishes. Trans. Ill. St. Acad. Sci. 23:219-226.

———
1942. Age determination and rate of growth of Polyodon spathula by means of the growth rings of the otoliths and dentary bone. Amer. Mid. Nat. 28:617-630.

Alexander, M. L.
1914. The paddlefish (Polyodon spathula) commonly called spoonbill cat. Trans. Amer. Fish. Soc. 44:73-78.

Allen, W. F.
1911. Notes on the breeding season and young of Polyodon spathula. Jour. Wash. Acad. Sci. 1:280-283.

Ariola, V.
1900. Rivisione della famiglia Bothriocephalidae, s. str. Arch. Parasitol. 3:369-484.

Barbour, T.
1911. The smallest Polyodon. Biol. Bull. 21:207-208.

Beach, H.
1902. The paddlefish Polyodon spathula. Bull. Wisc. Nat. Hist. Soc. 2:85-86.

Beaver, P. C. and Simer, P. H.
1940. A re-study of the three existing species of the cestode genus Marsipometra Cooper (Amphicotylidae) from the spoonbill Polyodon spathula (Wal.). Trans. Amer. Micr. Soc. 59:167-182.

Boyko, E. G.
1946. Age determination in fishes, based on examination of fin-ray sections (Translated title). Comptes Rendus, Academy of Science, Moskow, New Series 53:483-484. (Original available but not translated; reprinted in Prog. Fish Cult. 12:47-48).

Carlander, H. B.
1954. A history of fish and fishing in the upper Mississippi River. Upper Mississippi River Conservation Committee,

Iowa State Conservation Commission, Des Moines, Iowa.

Carlander, K. D.
1953. Handbook of freshwater fishery biology, with the first supplement. Wm. C. Brown Company, Dubuque, Iowa.

Chugunov, N. I.
1925. On the method of determination of age of sturgeons. Bull. of Fish. No. 11.

Cooper, A. R.
1917. A morphological study of bothriocephalid cestodes from fishes. Jour. Parasitol. 4:33-38.

_____
1918. North American Pseudophyllidean cestodes from fishes. Ill. Biol. Monogr. 4:1-243.

Cuerrir, J. P.
1951. The use of pectoral fin rays for determining age of sturgeons and other species of fish. Canad. Fish Cult. 11:10-17.

_____ and Roussow, G.
1951. Age and growth of lake sturgeon from Lake St. Francis, St. Lawrence River. Report on material collected in 1947. Canad. Fish Cult. 10:17-29.

Danforth, C. H.
1911. A 74 millimeter Polyodon. Biol. Bull. 20:201-204.

Dean, Bashford
1895. Fishes, living and fossil. Columbia University Biological Series 3. Macmillan and Company, New York. 1895.

Eddy, S. and Hodson, A. C.
1955. Taxonomic keys to the common animals of the North Central States. Burgess Publishing Company, Minneapolis, Minnesota.

_____ and Simer, P. H.
1929. Notes on the food of the paddlefish. Trans. Ill. St. Acad. Sci. 21:59-68.

Ekbaum, Ella
1937. On the maturation and hatching of the eggs of the cestode, Triaenophorus crassus Forel from Canadian fish. Jour. Parasitol. 23:293-295.

Essex, H. E.
1927a. Early development of Diphyllobothrium latum in northern Minnesota. Jour. Parasitol. 14:106-109.

_____
1927b. The structure and development of Corallobothrium with descriptions of two new fish tapeworms. Ill. Biol. Monogr. 11:255-328 or 11:1-74.

_____
1928. On the life history of Bothriocephalus cuspidatus Cooper 1917, a tapeworm from the walleyed pike. Trans. Amer. Micr. Soc. 47:348-355.

Forbes, S. A.
1878. The food of Illinois fishes. Bull. Ill. St. Lab. Nat. Hist. 1:71-89.

_____
1888a. Studies of the food of freshwater fishes. Bull. Ill. St. Lab. Nat. Hist. 2:433-473.

_____
1888b. On the food relations of freshwater fishes: a summary and discussion. Bull. Ill. St. Lab. Nat. Hist. 2:475-538.

_____ and Richardson, R. E.
1908. The fishes of Illinois. Ill. Nat. Hist. Surv. 3:15-20.

Graham, Michael
1929. Studies in the age determination of fish. Great Britain, Min. Agric. Fishery Div. Fisheries Ser. 2, 11:3-50.

Harlan, J. R. and Speaker, E. B.
1956. Iowa Fish and Fishing. 3rd ed., State of Iowa, 1956. State Conservation Commission, Des Moines, Iowa.

Heincke, F.
1904. Occurrence and distribution of the eggs, larvae and various age groups of the food fishes in the North Sea. Conseil Perm. Int. Expl. Mer., Rapp. et Prov. Verb., Gen. Rept. 1902-1904, Appendix E:1-39.

Herrick, C. J.
1922. An introduction to neurology. 3rd ed. Philadelphia. W. B. Saunders Company. 1922.

Hile, Ralph
1936. Age and growth of the cisco (Leucichthys artedi)(LeSueur) in the lakes of the northeastern highlands, Wisconsin. Bull. U.S. Bur. Fish. 48:209-317.

Holzmayer, H.
1924. Zur Altersbestimmung der Acipenseriden. Zool. Anz. 60:16-18.

Houser, A. and Bross, M.
1959. Observations on growth and reproduction of the paddlefish. Trans. Amer. Fish. Soc. 88:50-52.

Hussakop, L.
1910. The spoonbill fishery of the lower Mississippi. Trans. Amer. Fish. Soc. 40:245-248.

Imms, A. D.
1904. Notes on the gill rakers of the spoonbill sturgeon, Polyodon spathula. Proc. Zool. Soc. London 1904. 2:22-35.

Jordan, D. S. and Evermann, B. W.
1896. The fishes of North and Middle America. Smithsonian Institute. Bull. U.S. Nat'l. Museum 47:1-1240.

Kofoid, C. A.
1900. Notes on the natural history of Polyodon. Science 11:252.

Kuczkowski, S.
1925. Die Entwicklung im Genus Ichthyotaenia Lönnb. Ein Beitrag zur Cercomertheorie auf Grund experimenteller Untersuchungen. Bull. Intern. Acad. Polonaise. Science, Letters, Cracovie. Classe Science Mathematique - Naturelles, B.:423-446.

Lagler, K. F.
1956. Freshwater fishery biology. Wm. C. Brown Company, Dubuque, Iowa.

LeCren, E. D.
1947. The determination of the age and growth of the perch (Perca fluviatilis) from the opercular bone. Jour. Animal Ecol., 16:188-204.

———
1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). Jour. Animal Ecol., 20:201-219.

Li, H. C.
1929. The life histories of D. decipiens and D. erinacei. Amer. Jour. Hyg. 10:527-550.

Linton, E.
1898. Notes on Cestode parasites of fishes. Proc. U.S. Nat. Museum 20:423-456.

MacFarland, W. H.
1954. Report of the University of California Salton Sea Research Program. (Mimeo.) University of California, Berkeley.

Mattes, O.
1926. Zur Biologie der Larvenentwicklung von Fasciola hepatica, besonders über den Einfluss der Wasserstoffionenkonzentration auf das Ausschlüpfen der Miracidien. Zool. Anz. 69:138-156.

McDonald, M.
1939. A key to the species of Cyclops in Iowa. Trans. Iowa Acad. Sci. 46:373-381.

Menon, M. D.
1950. The use of bones, other than otoliths, in determining the age and growth rate of fishes. Jour. du Conseil 16:311-335.

Mohr, Erna
1927. Bibliographie der Altersund Wachstums-Bestimmung bei Fischen. Jour. du Conseil 2:236-258.

Mueller, J. F.
1935. A Diphyllobothrium from cats and dogs in the Syracuse region. Jour. Parasitol. 21:114-121.

———
1959a. The laboratory propagation of Spirometra mansonoides as an experimental tool. I. Collecting, incubation, and hatching of the eggs. Jour. Parasitol. 45:353-361.

———
1959b. The laboratory propagation of Spirometra mansonoides (Mueller, 1935) as an experimental tool. II. Culture and infection of the copepod host, and harvesting the procercoid. Trans. Amer. Micr. Soc. 78:245-255.

Muench, B.
1958. Quinaldine, A new anesthetic for fish. Prog. Fish Cult. 20:42-44.

Nachtrieb, H. F.
1910. The primitive pores of Polyodon spathula. Jour. Exp. Zool. 9:455-468.

Needham, J. G. et. al.
1937. Culture methods for invertebrate animals. Comstock Publishing Associates, Ithaca, New York. 1937.

_____ and Needham, P. R.
1955. A guide to the study of freshwater biology. Comstock Publishing Associates, Ithaca, New York. 1955.

Norris, H. W.
1923. On the function of the paddle of the paddlefish. Proc. Iowa Acad. Sci. 30:135-137.

Ogren, R. E.
1959. The hexacanth embryo of a dilepidid tapeworm. II. The epidermal glands and post-maturation changes. Jour. Parasitol. 45:575-579.

Onorato, A. R. and Stunkard, H. W.
1931. The effect of certain environmental factors on the development and hatching of the eggs of blook flukes. Biol. Bull. 61:120-132.

Pennak, R. W.
1953. Freshwater invertebrates of the United States. The Ronald Press Company, New York. 1953.

Probst, R. T. and Cooper, E. L.
1955. Age, growth, and production of the lake sturgeon (Acipenser fulvescens) in the Lake Winnebago Region, Wisconsin. Trans. Amer. Fish. Soc. 84:207-227.

Rafinesque, C. S.
1820. Fishes of the River Ohio. Western Review and Misc. Magazine. Lexington, Kentucky. Nov. 1820:244-252.

Redlich, E.
1925. Diaptomus graciloides (Lilljeborg), ein neuer erster Zwischenwirt von Dibothriocephalus latus, nebst Bermerkungen zur experimentellen Entwicklung des Procercoids

dieses Cestoden. Arch. Wiss. Prakt. Tierheilk. 53:353-361.

Reece, L.
1953. Transportation of marine fish. Outdoor California 14:4-5.

Rosen, F.
1918. Recherches sur le developpement des cestodes. I. Le cycle evolutif des Bothriocephales. Bull. Soc. Neuchatel sci. nat. 43:1-64.

Roussow, G.
1955a. Les esturgeons du fleuve Saint Laurent en comparaison avec les autres especes d' Acipenserides. Office de Biologie. Ministere de la Chasse et des Pecheries Province de Quebec. Montreal. 1955. (Mimeo.).

———
1955b. Quelques observations sur les variations de forme et de couleurchez les esturgeons de la province de Quebec. Annales de l'Acfas 21:79-85.

———
1957. Some considerations concerning sturgeon spawning periodicity. Jour. Fish. Res. Bd. Canada 14:553-572.

Rowan, W. B.
1956. The mode of hatching of the egg of Fasciola hepatica. Exp. Parasitol. V:118-137.

Schultz, F. H.
1956. Transfer of anaesthetized pike and yellow walleye. Canadian Fish Cult. No. 18:1-5.

Shields, J. T.
1958. Annual Report. South Dakota 1957-1958. Department of Game, Fish, and Parks, Pierre, South Dakota.

Simer, P. H.
1930. A preliminary study of the cestodes of the spoonbill, Polyodon spathula (Wal.). Trans. Ill. Acad. Sci. 22:139-145.

Smith, Ralph J.
1958. South Dakota's peculiar paddlefish. Sports Afield V. 139:48-49, 107-109.

Smyth, J. D.
1955. Problems relating to the in vitro cultivation of pseudophyllidean cestodes from egg to adult. Revista Iberica

de Parasitologia, Granada (Espana) Tomo Extraordinario, Marzo 1955:65-86.

St. Markowski
1935a. Über den Entwicklungszyklus von Bothriocephalus scorpii (Mueller 1776). Bull. Polska Akademija Umiejetnosci Krakow Series B. Sciences Naturelles II (1934-1935):1-17.

———
1935b. Einfluss der Milieuveränderungen auf die Entwicklung der Eier von Bothriocephalus scorpii (Mueller 1776). Bull. de l'Academie Polonaise des Sciences et des Lettres. Class des Sciences Mathematiques et Naturelles -- Series B: Sciences Naturelles II (1935) pp. 49-58.

Stockard, C. R.
1907. Observations on the natural history of Polyodon spathula. Amer. Nat. 41:753-766.

Stromsten, F. A.
1920a. Copepoda of the Okoboji region. Trans. Iowa Acad. Sci. Vol. 27:269-270.

———
1920b. Cladocera of the Okoboji region. Trans. Iowa Acad. Sci. Vol. 20:265-268.

Taylor, E. L.
1926. Observations on the hatching of a cestode egg. Ann. Trop. Med. and Parasitol. 20:220.

Thomas, A. P.
1883. The life history of the liver fluke (Fasciola hepatica). Quart. Jour. Micr. Sci. 23:99-133.

Thomas, L. J.
1929. Notes on the life history of Haplobothrium globuliforme Cooper, a tapeworm of Amia calva L. Jour. Parasitol. 16: 140-144.

———
1937. Environmental relationships and life histories of the tapeworm Bothriocephalus rarus. Jour. Parasitol. 23:133-150.

Thompson, D. H.
1933. The finding of very young Polyodon. Copeia 1933:31-33.

———
1934. Relative growth in Polyodon. Ill. Nat. Hist. Surv., Biology

Notes No. 2.

Ulmer, M. J.
1950. A critique of methods for the measurement of parasitic worms. Papers Michigan Acad. Sci., Arts, and Letters. 36:149-152.

Upper Mississippi River Conservation Committee
1958. Proc. of the 14th Annual Meeting, St. Paul, Minnesota, January 7, 1958. Iowa State Conservation Commission, Des Moines, Iowa.

Van Haitsma, J. P.
1931. Studies on the trematode family Strigeidae (Holostomidae). XXIII. Diplostomum flexicaudum (Cort and Brooks) and stages in its life history. Papers Michigan Acad. Sci., Arts, and Letters. 13:483-516.

Vergeer, T.
1936. The eggs and coracidia of Diphyllobothrium latum. Papers Michigan Acad. Sci., Arts, and Letters. 21:715-726.

Vogel, H.
1929. Studien zur Entwicklung von Diphyllobothrium. I. Teil: Die Wimperlarve von Diphyllobothrium latum. Zeitschrift für Wiss. Biol. Abt. F, Zeitschrift für Parasitenkunde, 2:213-222.

———
1930. Studien über die Entwicklung von Diphyllobothrium. II. Teil: Die Entwicklung des Procercoids von Diphyllobothrium latum. Zeitschrift für Wiss. Biol. Abt. F, Zeitschrift für Parasitenkunde, 2:629-654.

Walbaum, J. J.
1792. Petri artedi sueci genera piscium. Germany. Johanne Julio Walbaum. Grypeswaldiae.

Wardle, R. A. and McLeod, J. A.
1952. The Zoology of tapeworms. Published for the University of Manitoba by the University of Minnesota Press, Minneapolis.

Weed, A. C.
1925. Feeding the paddlefish. Copeia 146:67-68.

Wisniewski, L. W.
1933. Cyathocephalus truncatus Pallus. I. Die. Postembryonalen Entwicklung und Biologie. II. Allgemeine Morphologie. Polska Akademija Uniejetnosci Krakow. Bull. Int. Acad.

Polonais. Sci. Letters. Classe Sci. Math., Series B. Sci. Natu. II. (1932-1933):237-252, 311-327.

Yamaguti, S.
1959. Systema Helminthum. Vol. II. The Cestodes of Vertebrates. Interscience Publishers, Inc., New York.

ACKNOWLEDGMENTS

The author is especially grateful to Dr. Martin J. Ulmer for his patience, advice, and kind encouragement during the course of this investigation. Gratitude is also expressed to Dr. Kenneth D. Carlander for his interest, guidance, and assistance.

Appreciation is also expressed to the National Science Foundation, Washington, D. C. for providing the Fellowship which made this study possible.

Special thanks are due to Dr. Robert L. King, Director of the Iowa Lakeside Laboratory, for the use of laboratory space and equipment, and to James Sprague and J. T. Shields, biologists of the South Dakota Department of Game, Fish, and Parks for advice, assistance, and use of their specimens. Thanks are also due to the Kurrle and Mattson Fish Company, Burlington, Iowa and to the South Dakota Department of Game, Fish, and Parks for aid in collecting the paddlefish used in this study.

APPENDIX

Graphs and Plates

Abbreviations used:

C - cirrus

CM - circular muscles

CP - cirrus pouch

E - egg

ED - excretory duct

EH - embryonic hook

FC - flame cell

GA - genital atrium

LM - longitudinal muscle

LN - lateral nerve cord

O - ovary

PG - prostate gland

SR - seminal receptacle

SV - seminal vesicle

U - uterus

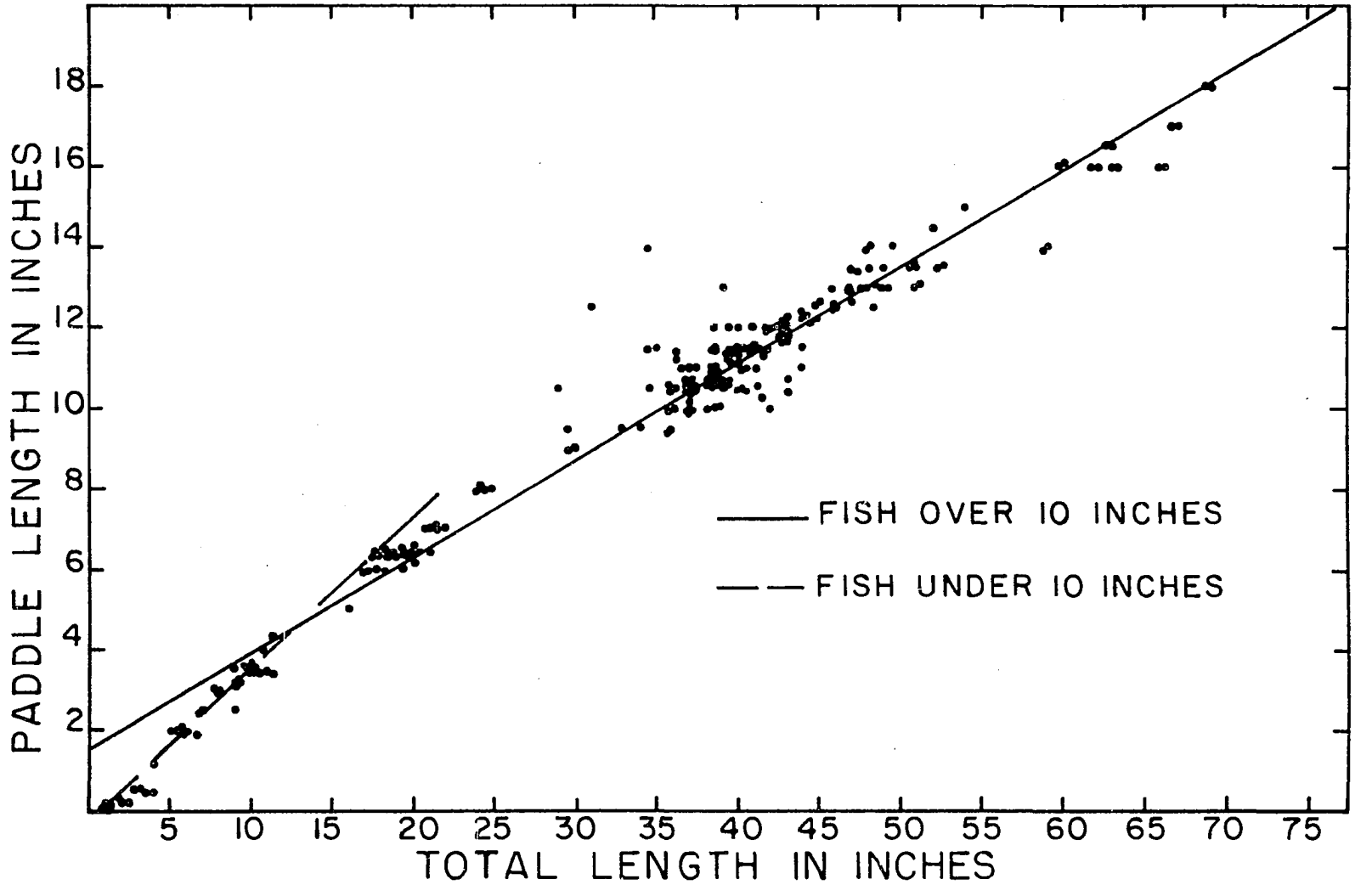
UP - uterine pore

V - vagina

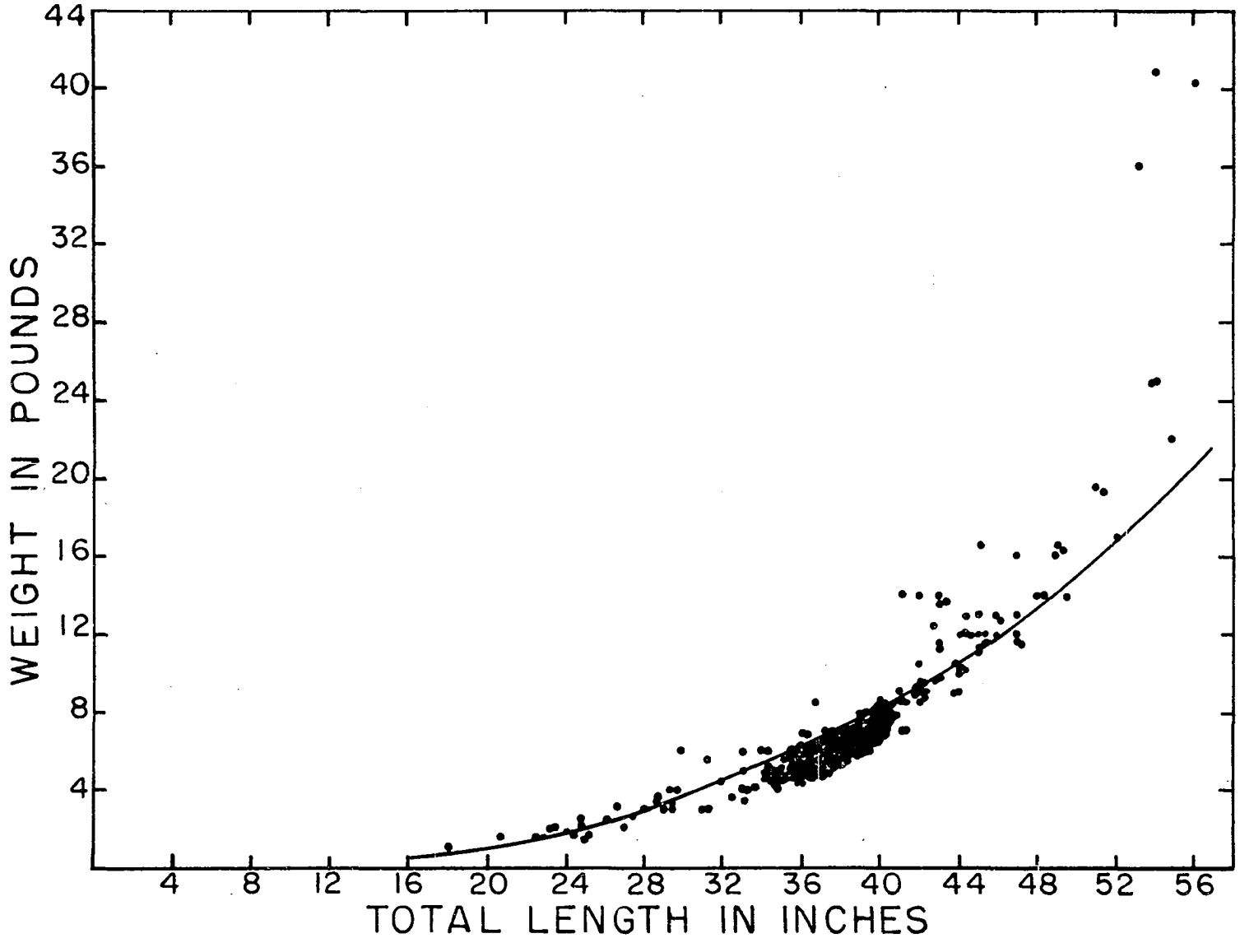
VD - vas deferens

VG - vitelline gland

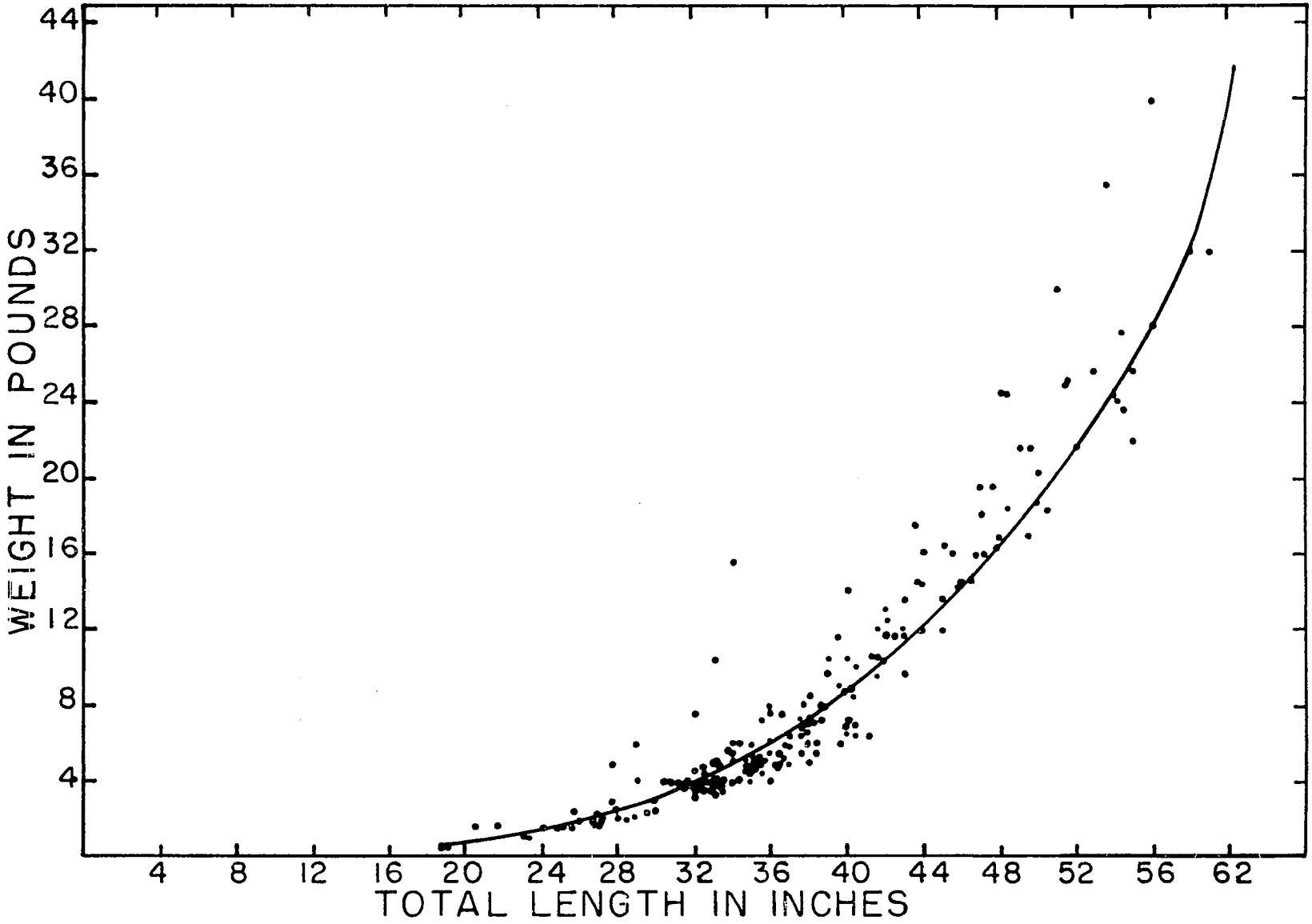
Graph 1. Relationship of paddle-length to total-length in paddlefish


PADDLE LENGTH IN INCHES
18
16
14
12
10
8
6
4
2
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
TOTAL LENGTH IN INCHES
FISH OVER 10 INCHES
FISH UNDER 10 INCHES

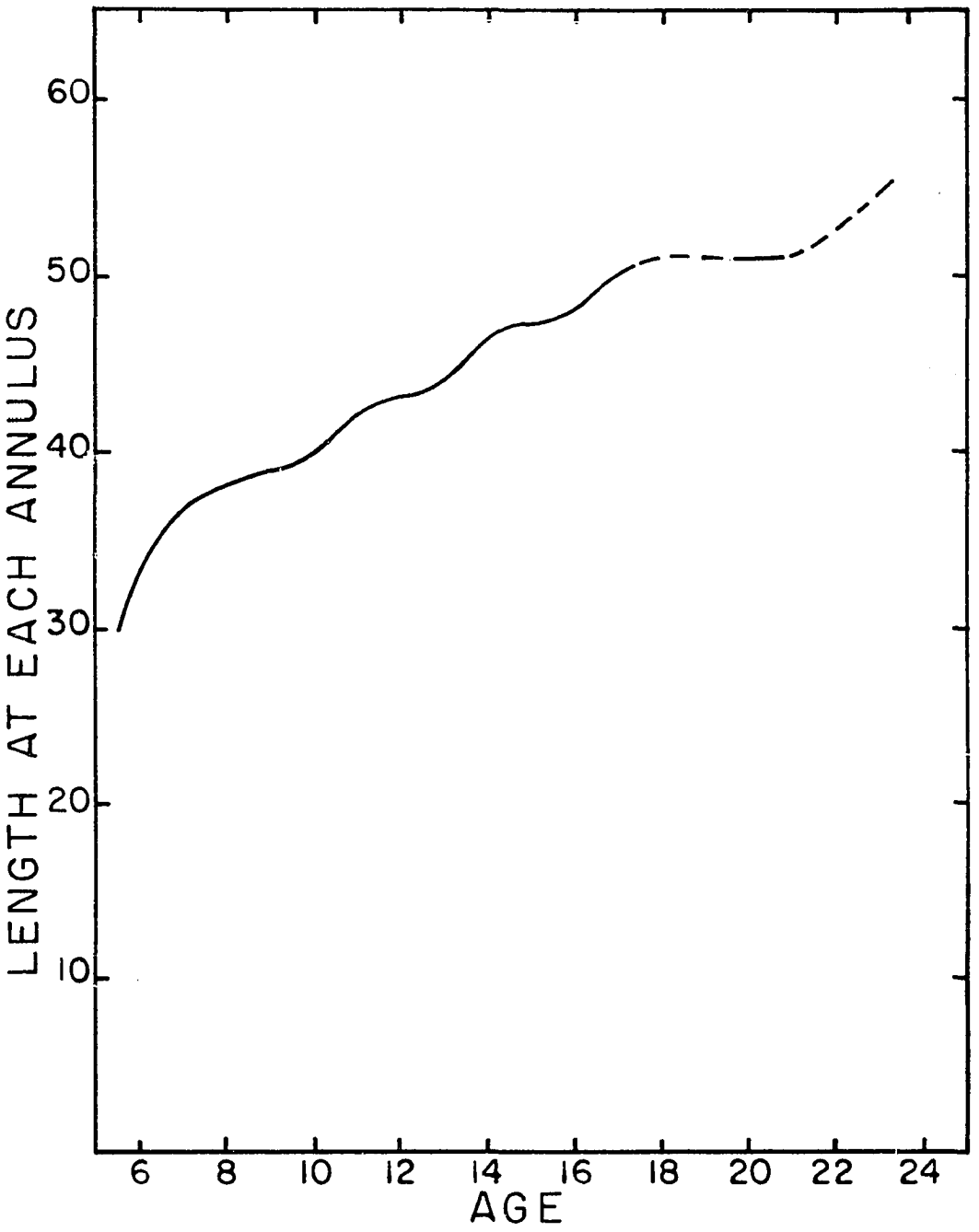
Graph 2. Length-weight relationship of paddlefish taken from the Mississippi River, 1958-1959


WEIGHT IN POUNDS
44
40
36
32
28
24
20
16
12
8
4
4 8 12 16 20 24 28 32 36 40 44 48 52 56
TOTAL LENGTH IN INCHES

Graph 3. Length-weight relationship of paddlefish taken from the Missouri River, 1958-1959

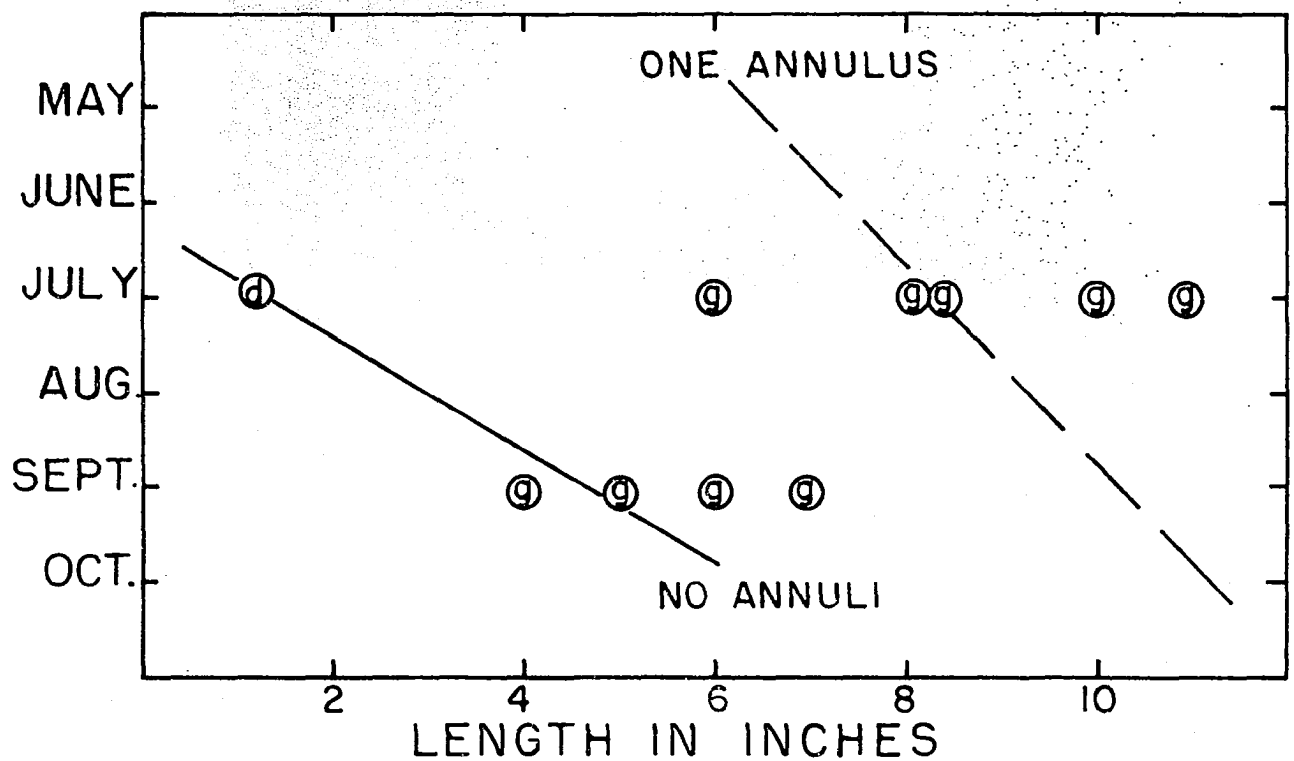

WEIGHT IN POUNDS
44
40
36
32
28
24
20
16
12
8
4
4 8 12 16 20 24 28 32 36 40 44 48 52 56 62
TOTAL LENGTH IN INCHES

Graph 4. Length-age relationship of paddlefish taken from the Mississippi River, 1958-1959


LENGTH AT EACH ANNULUS
60
50
40
30
20
10
6
8
10
12
14
16
18
20
22
24
AGE

Graph 5. Small Polyodon: collections made in Iowa from the Missouri River

d - Aitken, W., personal communication, 1958
g - Iowa State University Fish Collection


ONE ANNULUS
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NO ANNULI
2
4
6
8
10
LENGTH IN INCHES

Graph 6. Small Polyodon: collections made in Illinois and Missouri from the Mississippi River

a - Thompson, 1933
c - Barbour, 1911
e - Danforth, 1911
f - Allen, 1911

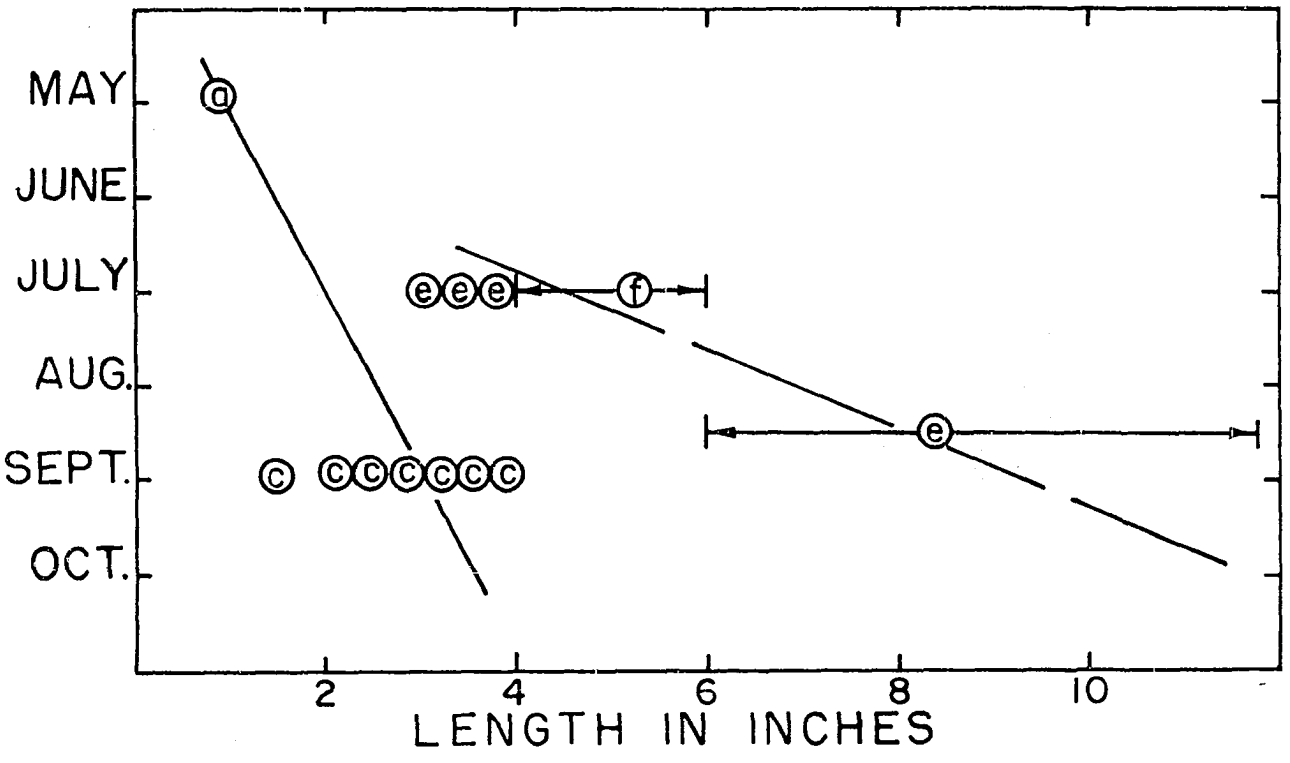

MAY
JUNE
JULY
AUG.
SEPT.
OCT.
2
4
6
8
10
LENGTH IN INCHES

PLATE I

Fig. 1. Coracidium of *Marsipometra hastata*

Fig. 2. Embryonic hook, free-hand drawing

Fig. 3. Largest plerocercoid recovered from haemocoel of *Cyclops bicuspidatus*

Fig. 4. Developing plerocercoids within the haemocoel of *C. bicuspidatus*, free-hand drawing

Fig. 5. Well-developed plerocercoid within haemocoel of *C. bicuspidatus*

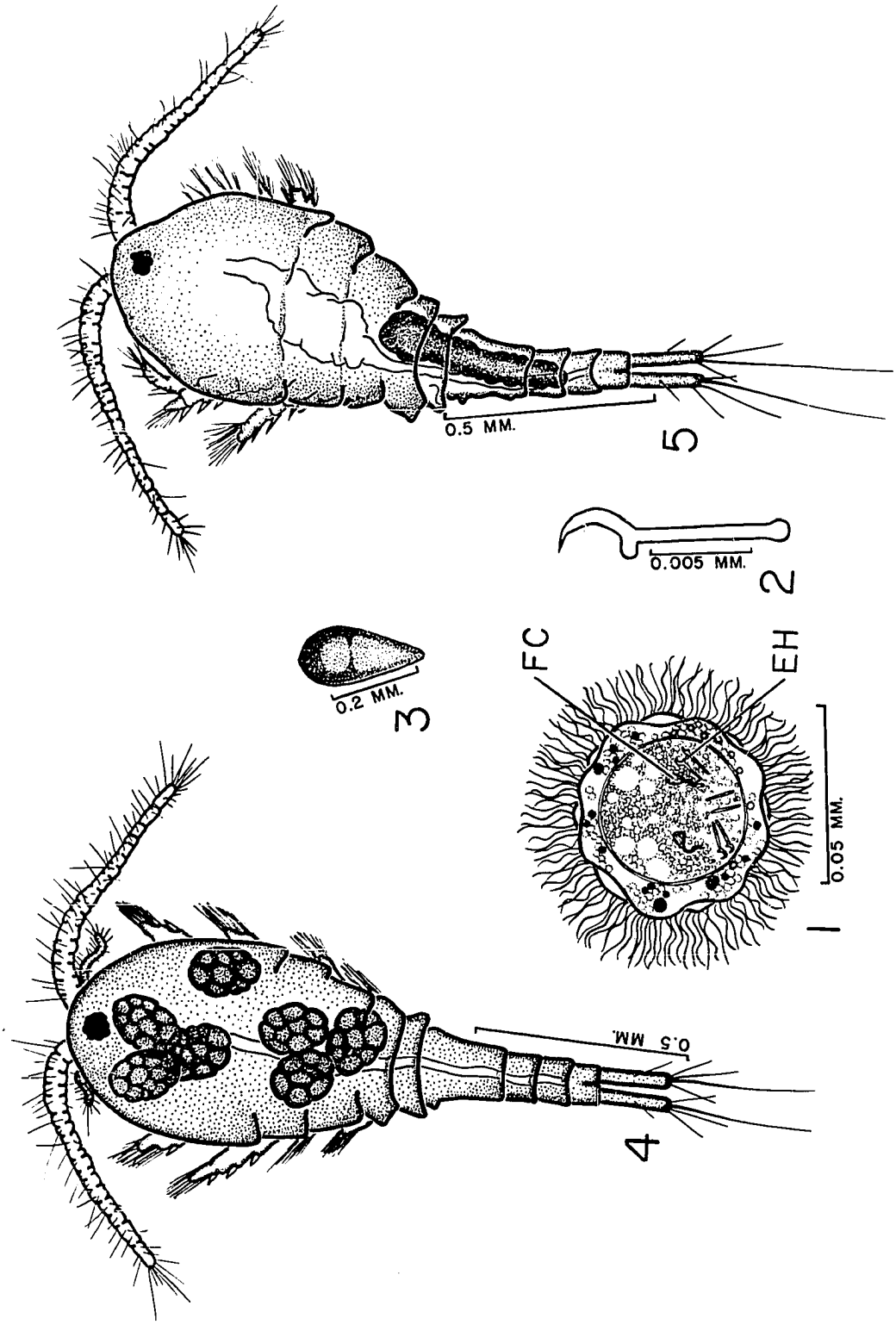
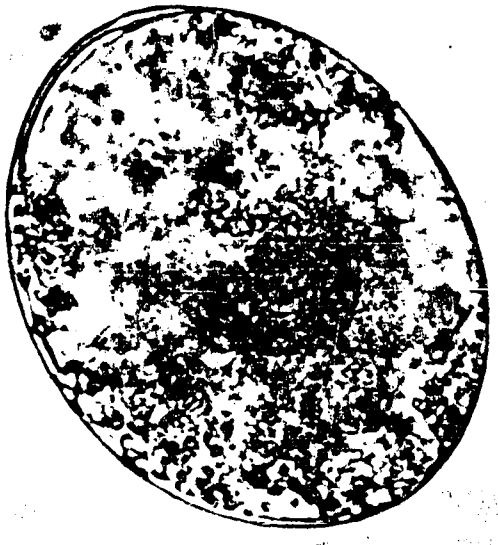

0.5 MM.
5
0.005 MM.
2
0.2 MM.
3
FC
EH
0.05 MM.
1
0.5 MM.
4

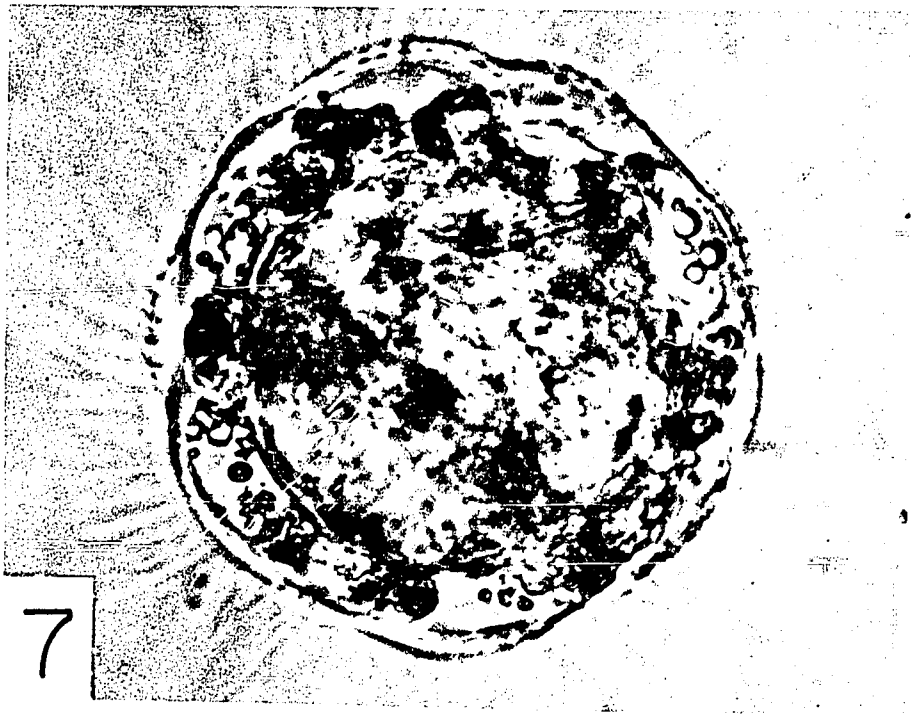
PLATE II

Fig. 6. Egg of Marsipometra hastata

Fig. 7. Newly emerged coracidium



6



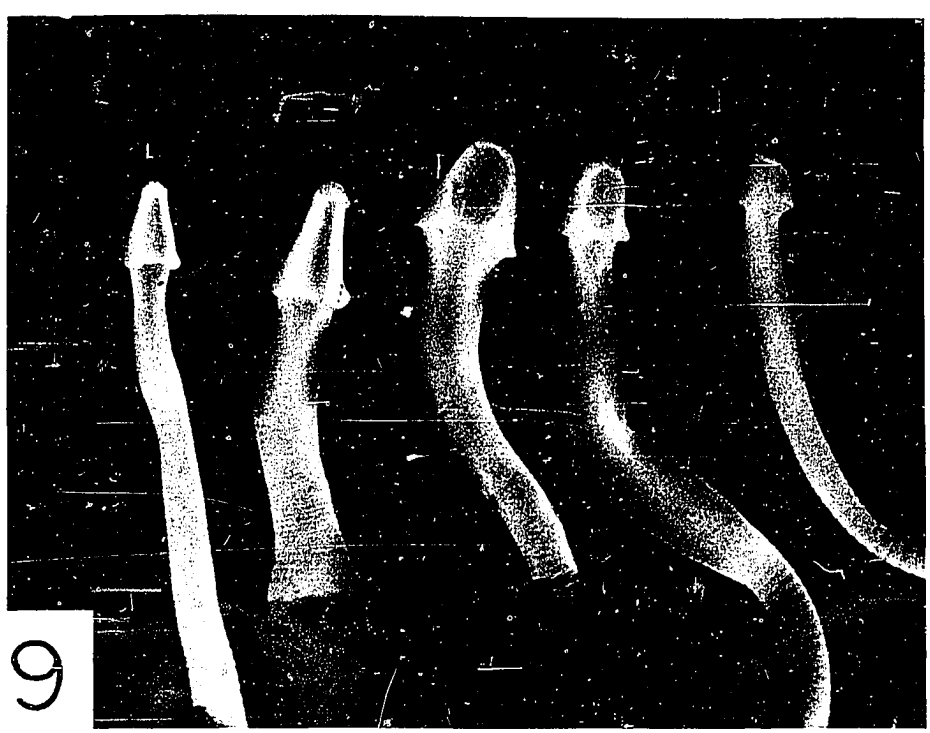
7

PLATE III

Fig. 8. Tapeworms *in situ* in the intestine of *Polyodon spathula*

Fig. 9. Scolices of living worms, showing variations in shape

8



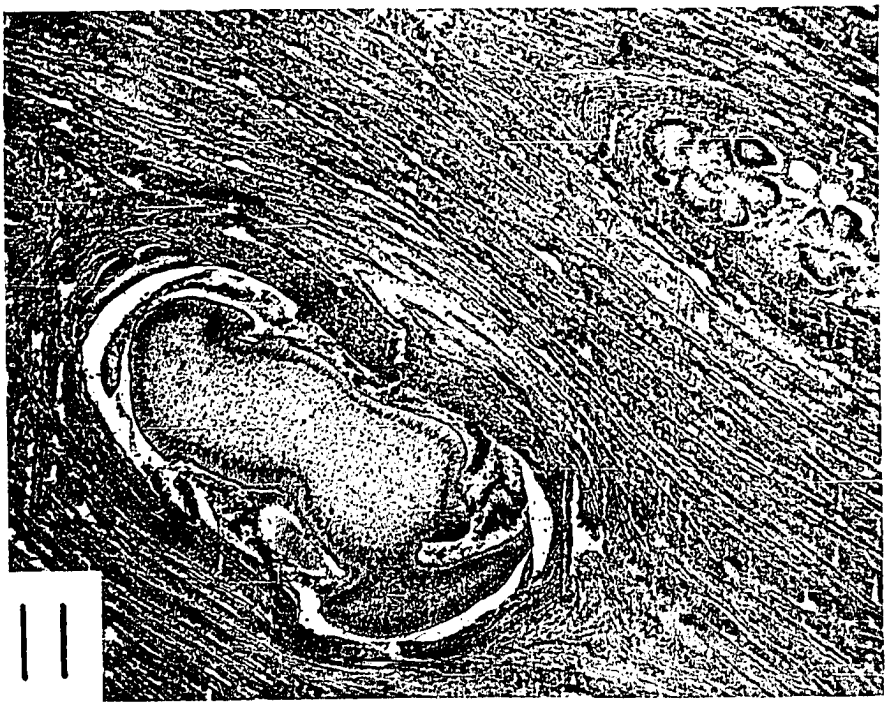
9

PLATE IV

Fig. 10. Cross-section of intestine of Polyodon spathula showing worms in situ

Fig. 11. Section of intestinal wall of P. spathula showing embedded scolex

10



11

PLATE V

Fig. 12. Smallest plerocercoid recovered from intestine of Polyodon spathula

Figs. 13-14. Small plerocercoids with developing post-holdfast regions

Fig. 15. Scolex of mature Marsipometra hastata

Figs. 16-17. Immature proglottids of M. hastata

Fig. 18. Mature proglottid

Fig. 19. Frontal section of mature proglottid

Figs. 20-21. Variations in the shape of uteri of gravid proglottids

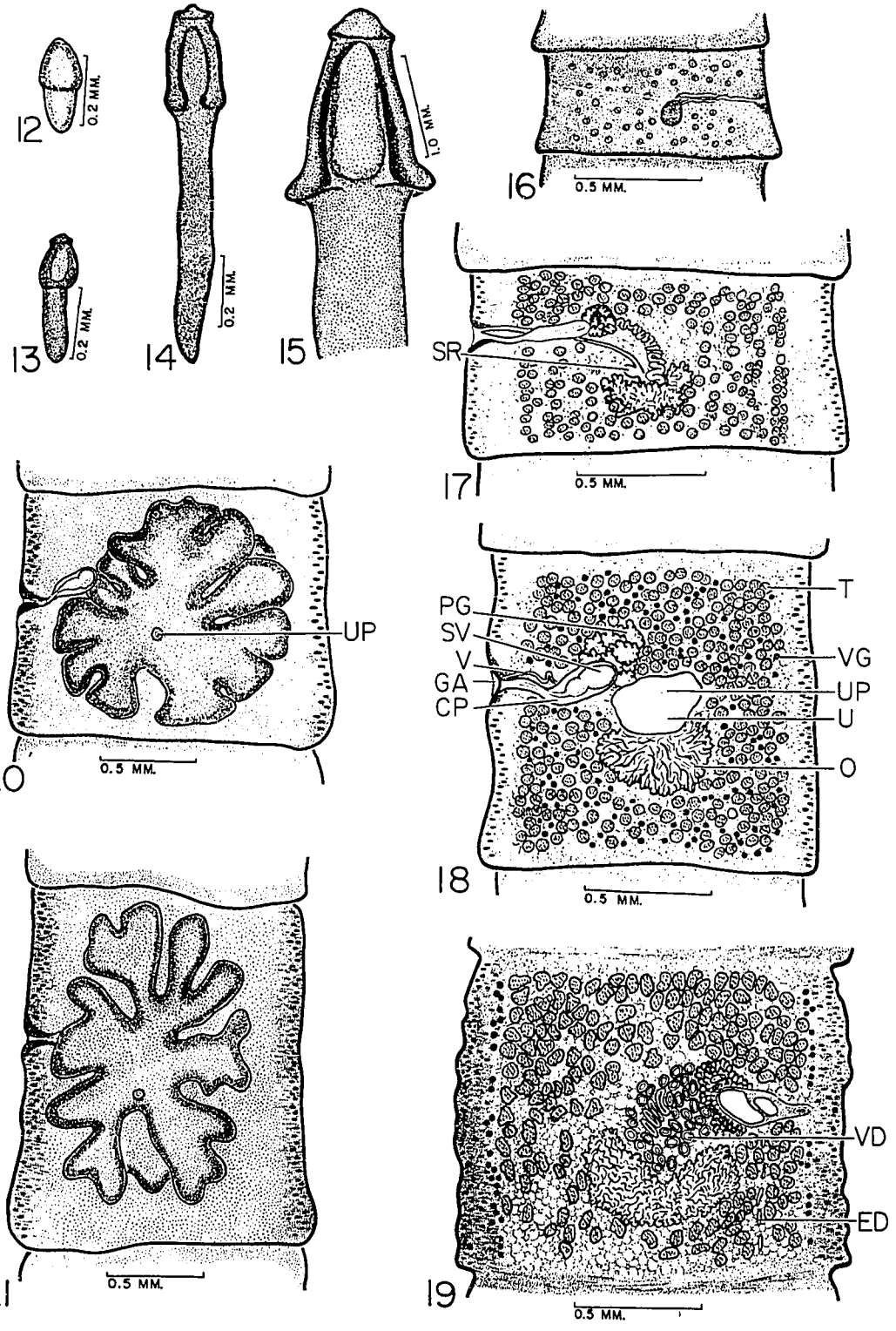
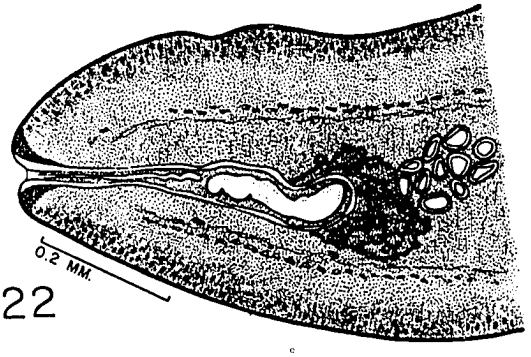

12
0.2 MM.
13
0.2 MM.
14
0.2 MM.
15
1.0 MM.
16
0.5 MM.
17
SR
0.5 MM.
18
PG
SV
V
GA
CP
T
VG
UP
U
O
0.5 MM.
19
VD
ED
0.5 MM.
20
UP
0.5 MM.
21
0.5 MM.

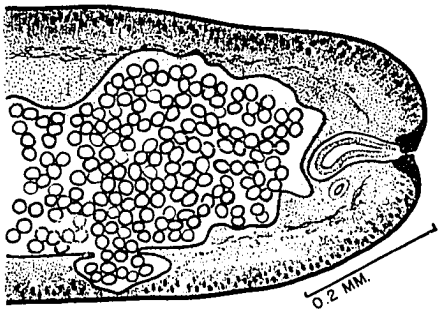
PLATE VI

Figs. 22-24. Cross-sections of mature proglottids from a single strobila showing variations in the depth of the genital atrium

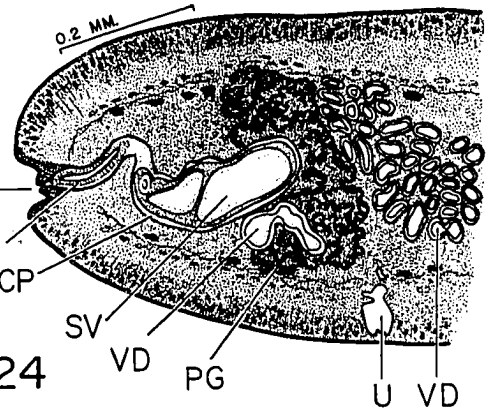
Figs. 25-27. Cross-sections of mature proglottids from a single strobila showing variations in the arrangement of testes



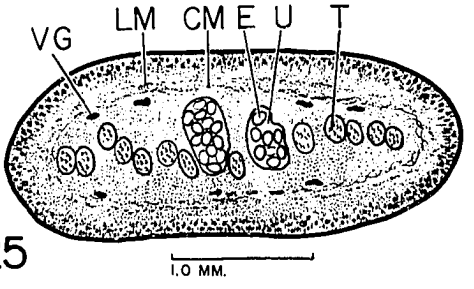
22



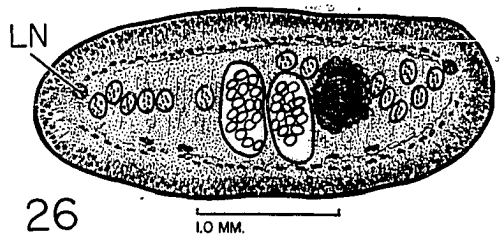
23



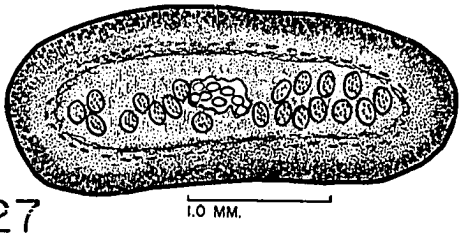
24



25



26



27

PLATE VII

Fig. 28. Nineteen inch specimen of *Polyodon spathula*

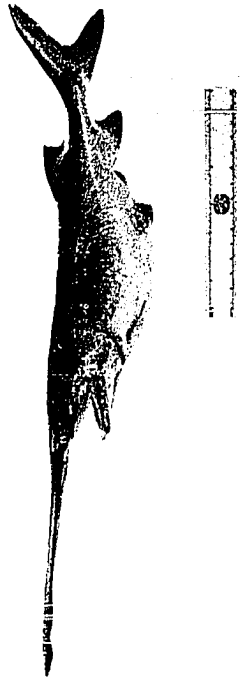
Fig. 29. Eight inch paddlefish collected from the Mississippi River, July, 1959

Fig. 30. Paddle of a large *Polyodon*

Fig. 31. Oral cavity of paddlefish showing gill arches

30

31



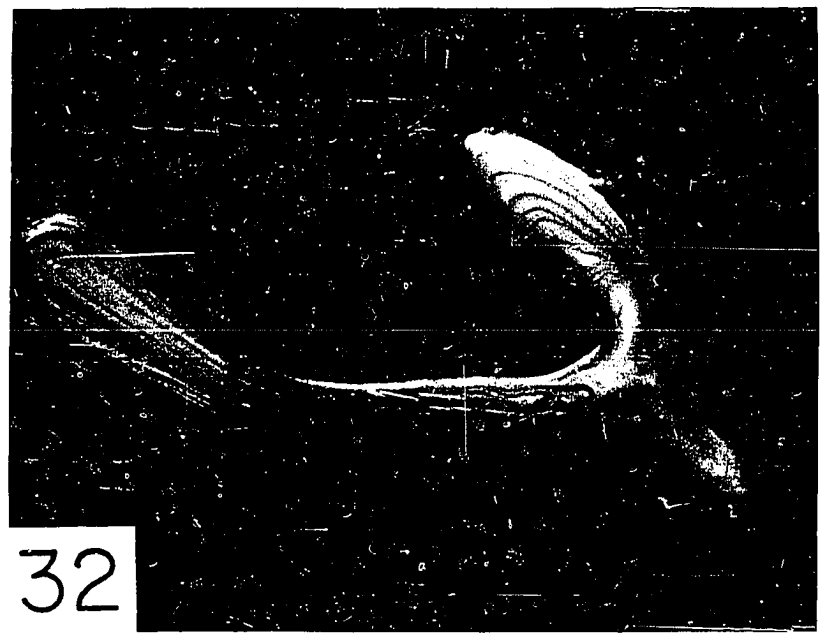
28

29

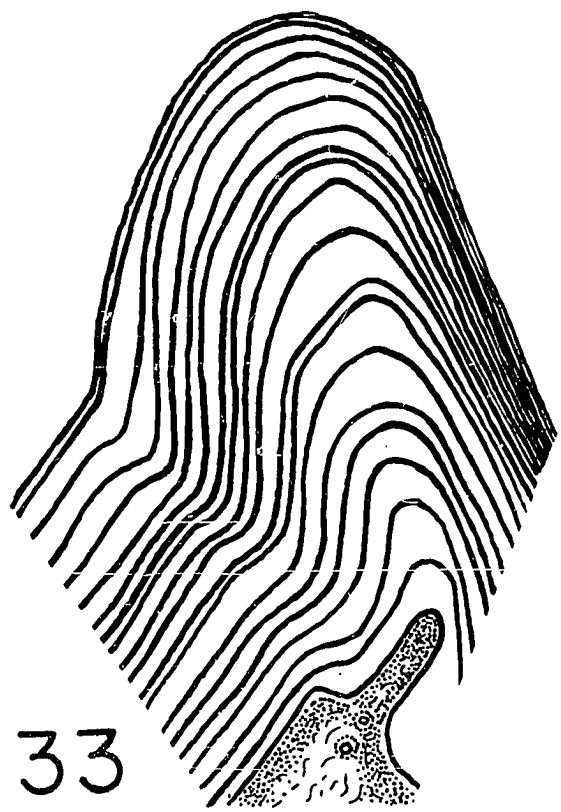
PLATE VIII

Fig. 32. Cross-section of dentary bone of a nine year-old paddlefish

Fig. 33. Cross-section of dentary bone showing annuli of a nineteen year-old paddlefish



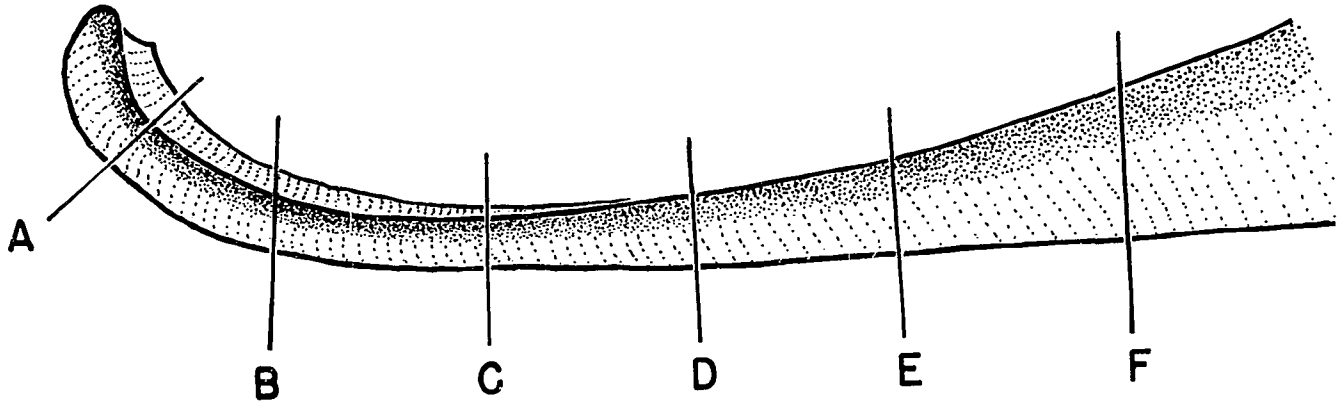
32

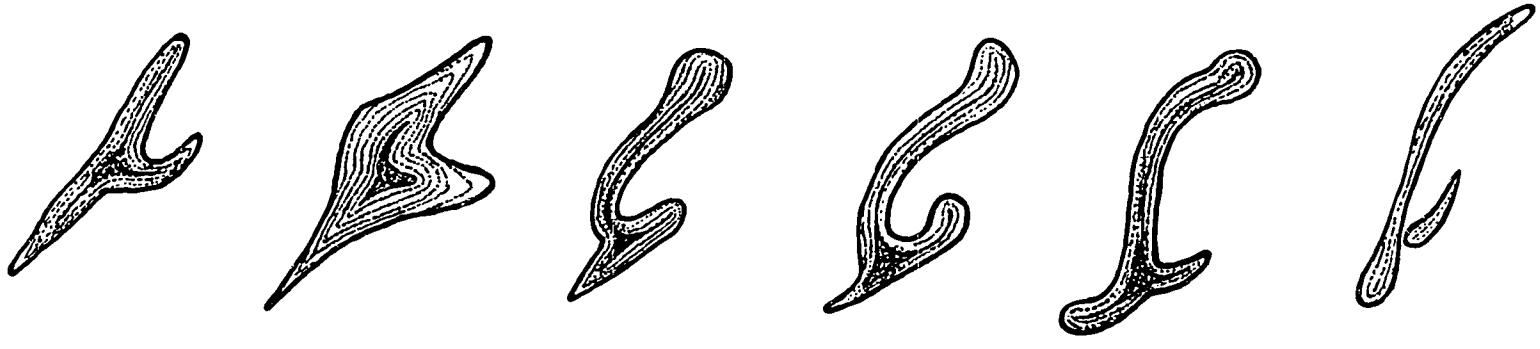


33

PLATE IX

Fig. 34. Variations in the shape of cross-sections of the dentary bone taken from different areas





34

PLATE X

Fig. 35. Ovaries of gravid Polyodon

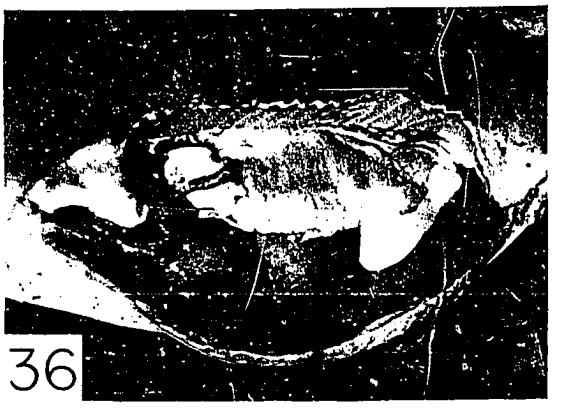
Fig. 36. Ovary of a sexually-inactive adult paddlefish

Fig. 37. Cross-section of ovary of a sexually inactive, small-sized adult paddlefish (low power)

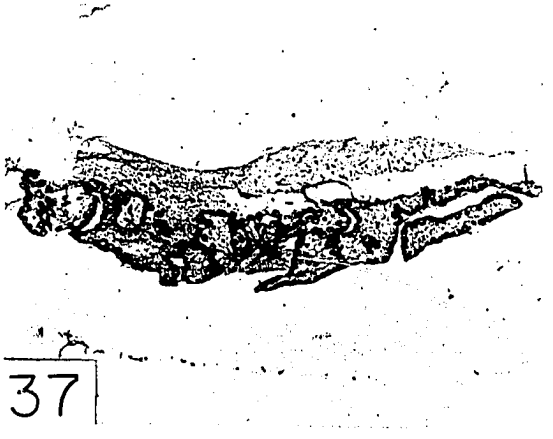
Fig. 38. Cross-section of ovary of a sexually inactive adult paddlefish of large size (low power)

Fig. 39. Cross-section of ovary from a sexually inactive adult paddlefish (high power)

35

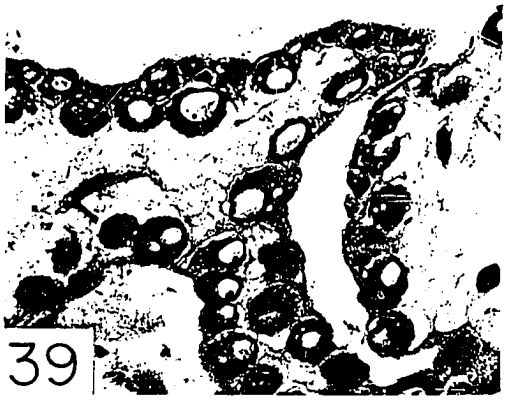


36



37

38



39

PLATE XI

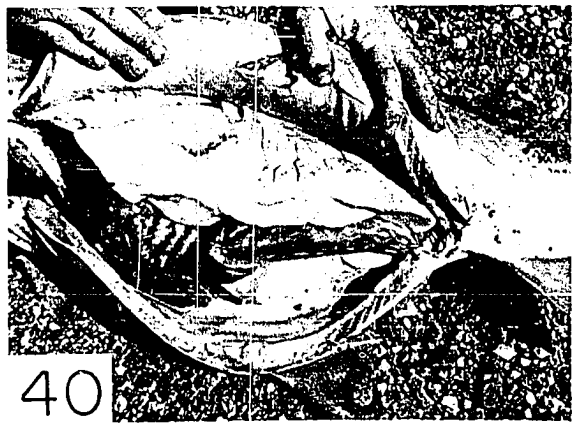
Fig. 40. Testis of adult paddlefish (low power)
Note massive fat body surrounding testis

Fig. 41. Cross-section of testis from sexually immature paddlefish (low power)

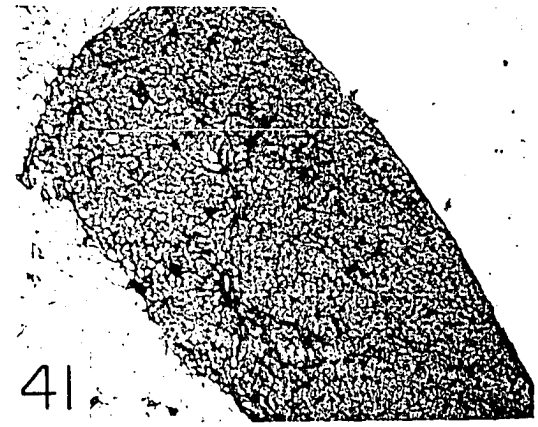
Fig. 42. Cross-section of testis from sexually immature paddlefish (high power)

Fig. 43. Cross-section of testis from adult paddlefish (low power)

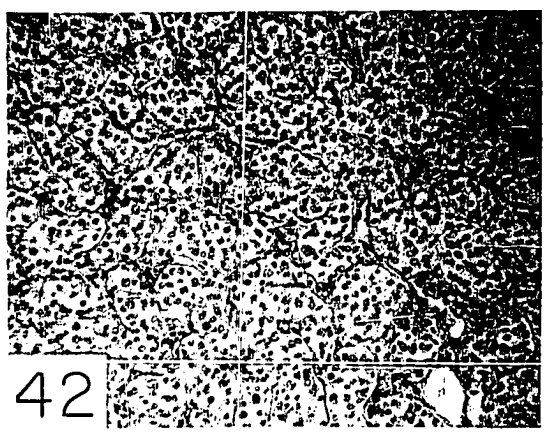
Fig. 44. Cross-section of testis from adult paddlefish (high power)



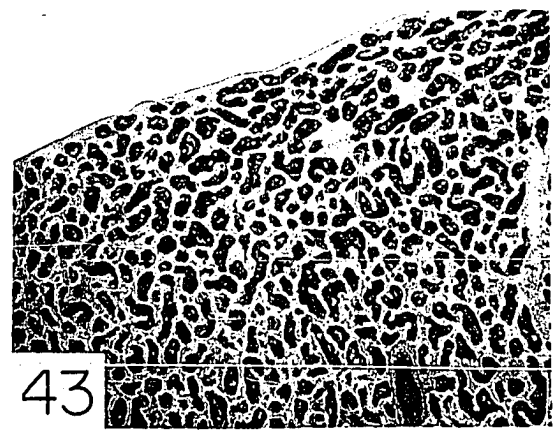
40



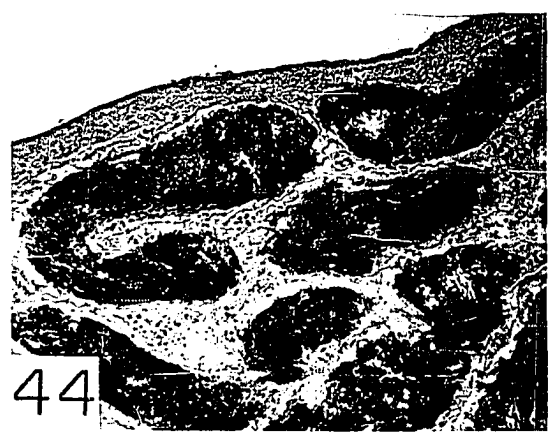
41



42



43



44